The Enzyme List
Class 3 — Hydrolases

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

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EC 3.1 Acting on ester bonds

This subclass contains the esterase enzymes. The esterases are subdivided into: carboxylic-ester hydrolases (EC 3.1.1), thioester hydrolases (EC 3.1.2), phosphoric-monoester hydrolases, the phosphatases (EC 3.1.3), phosphoric-diester hydrolases (EC 3.1.4), triphosphoric-monoester hydrolases (EC 3.1.5), sulfuric-ester hydrolases, the sulfatases (EC 3.1.6), diphosphoric monoesterases (EC 3.1.7) and phosphoric-triester hydrolases (EC 3.1.8). The nucleases, previously included under EC 3.1.4, are now placed in a number of new sub-subclasses: the exonucleases (EC 3.1.11-16) and the endonucleases (EC 3.1.21-31).!

EC 3.1.23 and EC 3.1.24

In a previous edition, site-specific endodeoxyribonucleases were set out individually in subclasses EC 3.1.23 and EC 3.1.24 (since deleted), with 113 separate entries. These are now included in three entries EC 3.1.21.3, EC 3.1.21.4 and EC 3.1.21.5. A complete listing of all of these enzymes has been produced by R.J. Roberts and is available at http://rebase.neb.com/rebase/rebase.html.

EC 3.1.1 Carboxylic-ester hydrolases

EC 3.1.1.1

Accepted name: carboxylesterase

Reaction: a carboxylic ester + H₂O = an alcohol + a carboxylate

Other name(s): ali-esterase; B-esterase; monobutyrase; cocaine esterase; procaine esterase; methylbutyrase; vitamin A esterase; butyryl esterase; carboxyesterase; carboxylate esterase; carboxylic esterase; methylbutyrate esterase; triacetin esterase; carboxyl ester hydrolase; butyrate esterase; methylbutyrase; α-carboxylesterase; propionyl esterase; nonspecific carboxylesterase; esterase D; esterase B; esterase A; serine esterase; carboxylic acid esterase; cocaine esterase

Systematic name: carboxylic-ester hydrolase

Comments: Wide specificity. The enzymes from microsomes also catalyse the reactions of EC 3.1.1.2 (arylesterase), EC 3.1.1.5 (lysophospholipase), EC 3.1.1.6 (acylesterase), EC 3.1.1.23 (acylglycerol lipase), EC 3.1.1.28 (acylcarnitine hydrolase), EC 3.1.2.2 (palmitoyl-CoA hydrolase), EC 3.5.1.4 (amidase) and EC 3.5.1.13 (aryl-acylamidase). Also hydrolyses vitamin A esters.

References: [82, 125, 184, 301, 1040, 1547, 1639, 2165]

[EC 3.1.1.1 created 1961]

EC 3.1.1.2

Accepted name: arylesterase

Reaction: a phenyl acetate + H₂O = a phenol + acetate

Other name(s): A-esterase; paraoxonase; aromatic esterase

Systematic name: aryl-ester hydrolase

Comments: Acts on many phenolic esters. The reactions of EC 3.1.8.1 arylalkylphosphatase, were previously attributed to this enzyme. It is likely that the three forms of human paraoxonase are lactonases rather than aromatic esterases [1244, 575]. The natural substrates of the paraoxonases are lactones [1244, 575], with (±)-5-hydroxy-6E,8Z,11Z,4Z-eicostetraenoic-acid 1,5-lactone being the best substrate [575].

References: [27, 87, 244, 1256, 1523, 1, 1244, 575]

[EC 3.1.1.2 created 1961, modified 1989]

EC 3.1.1.3

Accepted name: triacylglycerol lipase
Reaction: \( \text{triacylglycerol} + \text{H}_2\text{O} = \text{diacylglycerol} + \text{a carboxylate} \)

Other name(s): lipase; triglyceride lipase; tributyrase; butyrinase; glycerol ester hydrolase; tributyrinase; Tween hydrolase; steapsin; triacetinase; tributyrin esterase; Teevenase; amano N-AP; Takedo 1969-4-9; Meito MY 30; Tweenesterase; GA 56; capalase L; triglyceride hydrolase; triolein hydrolase; tween-hydrolyzing esterase; amano CE; cacordase; triglyceridase; triacylglycerol ester hydrolase; amano P; amano AP; PPL; glycerol-ester hydrolase; GEH; meito Sangyo OF lipase; hepatic lipase; lipazin; post-heparin plasma protamine-resistant lipase; salt-resistant post-heparin lipase; heparin releasable hepatic lipase; amano CES; amano B; tributyrase; triglyceride lipase; liver lipase; hepatic monoacylglycerol acyltransferase

Systematic name: triacylglycerol acylhydrolase

Comments: The pancreatic enzyme acts only on an ester-water interface; the outer ester links are preferentially hydrolysed.

References: [1309, 1517, 2207, 2336, 2337]

[EC 3.1.1.3 created 1961]

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EC 3.1.1.4

Accepted name: phospholipase A₂

Reaction: \( \text{phosphatidylcholine} + \text{H}_2\text{O} = \text{1-acylglycerophosphocholine} + \text{a carboxylate} \)

Other name(s): lecithinase A; phosphatidase; phosphatidolipase; phospholipase A

Systematic name: phosphatidylcholine 2-acylhydrolase

Comments: Also acts on phosphatidylethanolamine, choline plasmalogen and phosphatides, removing the fatty acid attached to the 2-position. Requires Ca²⁺.

References: [559, 718, 918, 1699, 2182, 2663]

[EC 3.1.1.4 created 1961, modified 1976, modified 1983]

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EC 3.1.1.5

Accepted name: lysophospholipase

Reaction: \( \text{2-lysophosphatidylcholine} + \text{H}_2\text{O} = \text{glycerophosphocholine} + \text{a carboxylate} \)

Other name(s): lecithinase B; lysolecithinase; phospholipase B; lysophosphatidase; lecitholipase; phosphatidase B; lysophosphatidylcholine hydrolase; lysosphospholipase A1; lysophospholipase t.2; lysophospholipase transacylase; neuropathy target esterase; NTE; NTE-LysoPLA; NTE-lysophospholipase

Systematic name: 2-lysophosphatidylcholine acylhydrolase

References: [5, 434, 491, 655, 2289, 2664, 2666, 2677, 2030, 1513, 2811]

[EC 3.1.1.5 created 1961, modified 1976, modified 1983]

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EC 3.1.1.6

Accepted name: acetyesterase

Reaction: \( \text{an acetic ester} + \text{H}_2\text{O} = \text{an alcohol} + \text{acetate} \)

Other name(s): C-esterase (in animal tissues); acetic ester hydrolase; chloroesterase; \( p\)-nitrophenyl acetate esterase; \textit{Citrus} acetyesterase

Systematic name: acetic-ester acetylhydrolase

References: [27, 176, 1133]

[EC 3.1.1.6 created 1961]

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EC 3.1.1.7

Accepted name: acetylcholinesterase

Reaction: \( \text{acetylcholine} + \text{H}_2\text{O} = \text{choline} + \text{acetate} \)

Other name(s): true cholinesterase; choline esterase I; cholinesterase; acetylthiocholinesterase; acetylcholine hydrolase; acetyl.β-methylcholinesterase; AcCholE
**Systematic name:** acetylcholine acetylhydrolase  
**Comments:** Acts on a variety of acetic esters; also catalyses transacetylations.  
**References:** [83, 177, 407, 1426, 1749, 2923]

[EC 3.1.1.7 created 1961]

**EC 3.1.1.8**  
**Accepted name:** cholinesterase  
**Reaction:** an acylcholine + H$_2$O = choline + a carboxylate  
**Other name(s):** pseudocholinesterase; butyrylcholine esterase; non-specific cholinesterase; choline esterase II (un-specific); benzoylcholinesterase; choline esterase; butyrylcholinesterase; propionylcholinesterase; anticholineesterase; BtChoEase  
**Systematic name:** acylcholine acylhydrolase  
**Comments:** Acts on a variety of choline esters and a few other compounds.  
**References:** [83, 87, 1295, 1749, 2224, 2435]

[EC 3.1.1.8 created 1961]

[3.1.1.9] **Deleted entry. benzoylcholinesterase; a side reaction of EC 3.1.1.8 cholinesterase**

[EC 3.1.1.9 created 1961, deleted 1972]

**EC 3.1.1.10**  
**Accepted name:** tropinesterase  
**Reaction:** atropine + H$_2$O = tropine + tropate  
**Other name(s):** tropine esterase; atropinase; atropine esterase;  
**Systematic name:** atropine acylhydrolase  
**Comments:** Also acts on cocaine and other tropine esters.  
**References:** [825, 1698]

[EC 3.1.1.10 created 1961, deleted 1972, reinstated 1976]

**EC 3.1.1.11**  
**Accepted name:** pectinesterase  
**Reaction:** pectin + $n$ H$_2$O = $n$ methanol + pectate  
**Other name(s):** pectin demethoxylase; pectin methoxylase; pectin methylesterase; pectase; pectin methyl esterase; pectinoesterase  
**Systematic name:** pectin pectylhydrolase  
**References:** [529, 1473, 1664]

[EC 3.1.1.11 created 1961]

[3.1.1.12] **Deleted entry. vitamin A esterase, now believed to be identical with EC 3.1.1.1 carboxylesterase**

[EC 3.1.1.12 created 1961, deleted 1972]

**EC 3.1.1.13**  
**Accepted name:** sterol esterase  
**Reaction:** a steryl ester + H$_2$O = a sterol + a fatty acid  
**Other name(s):** cholesterol esterase; cholesteryl ester synthase; triterpenol esterase; cholesteryl esterase; cholesteryl ester hydrolase; sterol ester hydrolase; cholesterol ester hydrolase; cholesterol ester hydrolase; cholesterol; acylcholesterol lipase  
**Systematic name:** steryl-ester acylhydrolase  
**Comments:** A group of enzymes of broad specificity, acting on esters of sterols and long-chain fatty acids, that may also bring about the esterification of sterols. Activated by bile salts.  
**References:** [1067, 1893, 2658, 2745]
EC 3.1.1.13

Accepted name: chlorophyllase
Reaction: chlorophyll + \( \text{H}_2\text{O} \rightarrow \text{phytol} + \text{chlorophyllide} 
Other name(s): CLH; Chlase
Systematic name: chlorophyll chlorophyllidohydrolase
Comments: Chlorophyllase has been found in higher plants, diatoms, and in the green algae *Chlorella* [2605]. This enzyme forms part of the chlorophyll degradation pathway and is thought to take part in degreening processes such as fruit ripening, leaf senescence and flowering, as well as in the turnover and homeostasis of chlorophyll [1894]. This enzyme acts preferentially on chlorophyll \( a \) but will also accept chlorophyll \( b \) and pheophytins as substrates [1042]. Ethylene and methyl jasmonate, which are known to accelerate senescence in many species, can enhance the activity of the hormone-inducible form of this enzyme [1042].

References: [1027, 1279, 2605, 1894, 1042]

EC 3.1.1.14

Accepted name: L-arabinonolactonase
Reaction: L-arabinono-1,4-lactone + \( \text{H}_2\text{O} \rightarrow \text{L-arabinonate} 
Systematic name: L-arabinono-1,4-lactone lactonohydrolase

References: [2771]

EC 3.1.1.15

Accepted name: D-glucurono-6,2-lactonase
Reaction: D-glucurono-1,5-lactone + \( \text{H}_2\text{O} \rightarrow \text{D-glucuronate} 
Systematic name: D-glucurono-1,5-lactone lactonohydrolase
Comments: Acts on a wide range of hexose-1,5-lactones. The hydrolysis of L-gulono-1,5-lactone was previously listed separately.

References: [275, 298, 2461]

EC 3.1.1.16

Deleted entry. 4-carboxymethyl-4-hydroxyisocrotonolactonase. This reaction was due to a mixture of EC 5.3.3.4 (muconolactone \( \Delta \)-isomerase) and EC 3.1.1.24 (3-oxoadipate enol-lactonase)

EC 3.1.1.17

Accepted name: glyconolactonase
Reaction: D-glucono-1,5-lactone + \( \text{H}_2\text{O} \rightarrow \text{D-gluconate} 
Other name(s): lactonase; aldolactonase; glucono-\( \delta \)-lactonase; gulonolactonase
Systematic name: D-glucono-1,5-lactone lactonohydrolase
Comments: Acts on a wide range of hexose-1,5-lactones. The hydrolysis of L-gulono-1,5-lactone was previously listed separately.

References: [275, 298, 2461]

EC 3.1.1.18

Deleted entry. aldolactonase. Now included with EC 3.1.1.17 glyconolactonase

EC 3.1.1.19

Accepted name: uronolactonase
Reaction: D-glucurono-6,2-lactone + \( \text{H}_2\text{O} \rightarrow \text{D-glucuronate} 
Systematic name: D-glucurono-6,2-lactone lactonohydrolase

References: [2809]

[EC 3.1.1.13 created 1961, modified 1990]
EC 3.1.1.20

Accepted name: tannase
Reaction: digallate + $\text{H}_2\text{O} = 2$ gallate
Other name(s): tannase S; tannin acetylhydrolase
Systematic name: tannin acylhydrolase
Comments: Also hydrolyses ester links in other tannins.
References: [601]

[EC 3.1.1.20 created 1961]

EC 3.1.1.21

Accepted name: retinyl-palmitate esterase
Reaction: retinyl palmitate + $\text{H}_2\text{O} = \text{retinol} + \text{palmitate}$
Other name(s): retinyl palmitate hydrolase; retinyl palmitate hydrolyase; retinyl ester hydrolase
Systematic name: retinyl-palmitate palmitohydrolase
References: [1528]

[EC 3.1.1.21 created 1972]

EC 3.1.1.22

Accepted name: hydroxybutyrate-dimer hydrolase
Reaction: $((\text{R})-3-((\text{R})-3\text{-hydroxybutanoyloxy})\text{butanoate} + \text{H}_2\text{O} = 2 (\text{R})-3\text{-hydroxybutanoate}$
Other name(s): $\text{D}(-)-3\text{-hydroxybutyrate-dimer hydrolase}$
Systematic name: $(\text{R})-3-((\text{R})-3\text{-hydroxybutanoyloxy})\text{butanoate hydroxybutanoylehydrolase}$
References: [513]

[EC 3.1.1.22 created 1972]

EC 3.1.1.23

Accepted name: acylglycerol lipase
Reaction: Hydrolyses glycerol monoesters of long-chain fatty acids
Other name(s): monoacylglycerol lipase; monoacylglycerolipase; monoglyceride lipase; monoglyceride hydrolase; fatty acyl monoester lipase; monoacylglycerol hydrolase; monoglyceridyllipase; monoglyceridase
Systematic name: glycerol-ester acylhydrolase
References: [1637, 2005]

[EC 3.1.1.23 created 1972]

EC 3.1.1.24

Accepted name: 3-oxoadipate enol-lactonase
Reaction: $3\text{-oxoadipate enol-lactone} + \text{H}_2\text{O} = 3\text{-oxoadipate}$
Other name(s): carboxymethylbutenolide lactonase; $\beta$-ketoadipic enol-lactone hydrolase; 3-ketoadipate enol-lactonase; 3-oxoadipic enol-lactone hydrolase; $\beta$-ketoadipate enol-lactone hydrolase
Systematic name: 4-carboxymethylbut-3-en-4-olide enol-lactonohydrolase
Comments: The enzyme acts on the product of EC 4.1.1.44 4-carboxymuconolactone decarboxylase.
References: [1909, 1910]

[EC 3.1.1.24 created 1961 as EC 3.1.1.16, part transferred 1972 to EC 3.1.1.24]

EC 3.1.1.25

Accepted name: 1,4-lactonase
Reaction: a 1,4-lactone + $\text{H}_2\text{O} = \text{a 4-hydroxyacid}$
Other name(s): γ-lactonase
Systematic name: 1,4-lactone hydroxyacylhydrolase
Comments: The enzyme is specific for 1,4-lactones with 4-8 carbon atoms. It does not hydrolyse simple aliphatic esters, acetylcholine, sugar lactones or substituted aliphatic lactones, e.g. 3-hydroxy-4-butyrolactone; requires Ca$^{2+}$.
References: [693, 694]

[EC 3.1.1.25 created 1972, modified 1981]

EC 3.1.1.26
Accepted name: galactolipase
Reaction: 1,2-diacyl-3-β-D-galactosyl-sn-glycerol + 2 H$_2$O = 3-β-D-galactosyl-sn-glycerol + 2 carboxylates
Other name(s): galactolipid lipase; polygalactolipase; galactolipid acylhydrolase
Systematic name: 1,2-diacyl-3-β-D-galactosyl-sn-glycerol acylhydrolase
Comments: Also acts on 2,3-di-O-acyl-1-O-(6-O-α-D-galactosyl-β-D-galactosyl)-D-glycerol, and phosphatidylcholine and other phospholipids.
References: [976, 1014]

[EC 3.1.1.26 created 1972]

EC 3.1.1.27
Accepted name: 4-pyridoxolactonase
Reaction: 4-pyridoxolactone + H$_2$O = 4-pyridoxate
Systematic name: 4-pyridoxolactone lactonohydrolase
References: [303]

[EC 3.1.1.27 created 1972]

EC 3.1.1.28
Accepted name: acylcarnitine hydrolase
Reaction: O-acylcarnitine + H$_2$O = a fatty acid + L-carnitine
Other name(s): high activity acylcarnitine hydrolase; HACH; carnitine ester hydrolase; palmitoylcarnitine hydrolase; palmitoyl-L-carnitine hydrolase; long-chain acyl-L-carnitine hydrolase; palmitoyl carnitine hydrolase
Systematic name: O-acylcarnitine acylhydrolase
Comments: Acts on higher fatty acid (C$_6$ to C$_{18}$) esters of L-carnitine; highest activity is with O-decanoyl-L-carnitine.
References: [1529, 1638]

[EC 3.1.1.28 created 1972]

EC 3.1.1.29
Accepted name: aminoacyl-tRNA hydrolase
Reaction: N-Substituted aminoacyl-tRNA + H$_2$O = N-substituted amino acid + tRNA
Other name(s): aminoacyl-transfer ribonucleate hydrolase; N-substituted aminoacyl transfer RNA hydrolase; peptidyl-tRNA hydrolase
Systematic name: aminoacyl-tRNA aminoacylhydrolase
References: [1163]

[EC 3.1.1.29 created 1972]

EC 3.1.1.30
Accepted name: D-arabinonolactonase
**Reaction:** D-arabinono-1,4-lactone + H₂O = D-arabinonate

**Systematic name:** D-arabinono-1,4-lactone lactonohydrolase

**References:** [1932]

[EC 3.1.1.30 created 1972]

**EC 3.1.1.31**

**Accepted name:** 6-phosphogluconolactonase

**Reaction:** 6-phospho-D-glucono-1,5-lactone + H₂O = 6-phospho-D-gluconate

**Other name(s):** phosphogluconolactonase; 6-PGL

**Systematic name:** 6-phospho-D-glucono-1,5-lactone lactonohydrolase

**References:** [1217, 1654]

[EC 3.1.1.31 created 1972]

**EC 3.1.1.32**

**Accepted name:** phospholipase A₁

**Reaction:** phosphatidylcholine + H₂O = 2-acylglycerophosphocholine + a carboxylate

**Systematic name:** phosphatidylcholine 1-acylhydrolase

**Comments:** This enzyme has a much broader specificity than EC 3.1.1.4 phospholipase A₂. Requires Ca²⁺.

**References:** [787, 2225, 2663, 2665]

[EC 3.1.1.32 created 1972, modified 1976]

**EC 3.1.1.33**

**Accepted name:** 6-acetylglucose deacetylase

**Reaction:** 6-acetyl-D-glucose + H₂O = D-glucose + acetate

**Other name(s):** 6-O-acetylglucose deacetylase

**Systematic name:** 6-acetyl-D-glucose acetylhydrolase

**References:** [592]

[EC 3.1.1.33 created 1972]

**EC 3.1.1.34**

**Accepted name:** lipoprotein lipase

**Reaction:** triacylglycerol + H₂O = diacylglycerol + a carboxylate

**Other name(s):** clearing factor lipase; diglyceride lipase; diacylglycerol lipase; postheparin esterase; diglyceride lipase; postheparin lipase; diacylglycerol hydrolase; lipemia-clearing factor

**Systematic name:** triacylglycerol-protein acylhydrolase

**Comments:** Hydrolyses triacylglycerols in chylomicrons and low-density lipoproteins. Also hydrolyses diacylglycerol.

**References:** [610, 683, 868, 1715, 1810]

[EC 3.1.1.34 created 1972, modified 1976]

**EC 3.1.1.35**

**Accepted name:** dihydrocoumarin hydrolase

**Reaction:** dihydrocoumarin + H₂O = melilotate

**Systematic name:** dihydrocoumarin lactonohydrolase

**Comments:** Also hydrolyses some other benzenoid 1,4-lactones.

**References:** [1316]
EC 3.1.1.36
Accepted name: limonin-D-ring-lactonase
Reaction: limonoate D-ring-lactone + H$_2$O = limonoate
Other name(s): limonin-D-ring-lactone hydrolase; limonin lactone hydrolase
Systematic name: limonoate-D-ring-lactone lactonohydrolase
Comments: Limonoate is a triterpenoid.
References: [1533]

EC 3.1.1.37
Accepted name: steroid-lactonase
Reaction: testololactone + H$_2$O = testolate
Systematic name: testololactone lactonohydrolase
References: [1029]

EC 3.1.1.38
Accepted name: triacetate-lactonase
Reaction: triacetate lactone + H$_2$O = triacetate
Other name(s): triacetate lactone hydrolase; triacetic acid lactone hydrolase; TAL hydrolase; triacetate lactone hydrolase
Systematic name: triacetolactone lactonohydrolase
References: [1215]

EC 3.1.1.39
Accepted name: actinomycin lactonase
Reaction: actinomycin + H$_2$O = actinomycinic monolactone
Systematic name: actinomycin lactonohydrolase
References: [1045]

EC 3.1.1.40
Accepted name: orsellinate-depside hydrolase
Reaction: orsellinate depside + H$_2$O = 2 orsellinate
Other name(s): lecanorate hydrolase
Systematic name: orsellinate-depside hydrolase
Comments: The enzyme will only hydrolyse those substrates based on the 2,4-dihydroxy-6-methylbenzoate structure that also have a free hydroxy group ortho to the depside linkage.
References: [2261]

EC 3.1.1.41
Accepted name: cephalosporin-C deacetylase
Reaction: cephalosporin C + H$_2$O = deacetylcephalosporin C + acetate
**Other name(s):** cephalosporin C acetyl-hydrolase; cephalosporin C acetylase; cephalosporin acetyl-esterase; cephalosporin C acetyl-esterase; cephalosporin C acetyl-esterase; cephalosporin C deacylase

**Systematic name:** cephalosporin-C acetylhydrolase

**Comments:** Hydrolyses the acetyl ester bond on the 10-position of the antibiotic cephalosporin C.

**References:** [756]

[EC 3.1.1.41 created 1976]

**EC 3.1.1.42**

**Accepted name:** chlorogenate hydrolase

**Reaction:** chlorogenate + H₂O = caffeate + quinate

**Other name(s):** chlorogenase; chlorogenic acid esterase

**Systematic name:** chlorogenate hydrolase

**Comments:** Also acts, more slowly, on isochlorogenate. No other substrates are known.

**References:** [2253, 2254]

[EC 3.1.1.42 created 1981]

**EC 3.1.1.43**

**Accepted name:** α-amino-acid esterase

**Reaction:** an α-amino acid ester + H₂O = an α-amino acid + an alcohol

**Other name(s):** α-amino acid ester hydrolase

**Systematic name:** α-amino-acid-ester aminoacylhydrolase

**Comments:** Also catalyses α-aminoacyl transfer to a number of amine nucleophiles.

**References:** [1213, 1214, 2493]

[EC 3.1.1.43 created 1983]

**EC 3.1.1.44**

**Accepted name:** 4-methyloxaloacetate esterase

**Reaction:** oxaloacetate 4-methyl ester + H₂O = oxaloacetate + methanol

**Systematic name:** oxaloacetate-4-methyl-ester oxaloacetohydrolase

**References:** [569]

[EC 3.1.1.44 created 1983]

**EC 3.1.1.45**

**Accepted name:** carboxymethylenebutenolidase

**Reaction:** 4-carboxymethylenebut-2-en-4-olide + H₂O = 4-oxohex-2-enediolate

**Other name(s):** maleylacetate enol-lactonase; dienelactone hydrolase; carboxymethylene butenolide hydrolase

**Systematic name:** 4-carboxymethylenebut-2-en-4-olide lactonohydrolase

**References:** [2248]

[EC 3.1.1.45 created 1983]

**EC 3.1.1.46**

**Accepted name:** deoxylimonate A-ring-lactonase

**Reaction:** deoxylimonate + H₂O = deoxylimononic acid D-ring-lactone

**Systematic name:** deoxylimonate A-ring-lactonohydrolase

**Comments:** The enzyme opens the A-ring-lactone of the triterpenoid deoxylimononic acid, leaving the D-ring-lactone intact.

**References:** [940]
EC 3.1.1.46

Accepted name: 1-alkyl-2-acetyl-sn-glycerophosphocholine esterase
Reaction: 1-alkyl-2-acetyl-sn-glycero-3-phosphocholine + H\textsubscript{2}O = 1-alkyl-sn-glycero-3-phosphocholine + acetate
Other name(s): 1-alkyl-2-acetyl-sn-glycero-3-phosphocholine acetylhydrolase; alkylacetyl-GPC:acetylhydrolase
Systematic name: 1-alkyl-2-acetyl-sn-glycero-3-phosphocholine acetoxydrolase
References: [219]

EC 3.1.1.47

Accepted name: fusarinine-C ornithinesterase
Reaction: \(N^5\)-acyl-L-ornithine ester + H\textsubscript{2}O = \(N^5\)-acyl-L-ornithine + an alcohol
Other name(s): ornithine esterase; 5-\(N\)-acyl-L-ornithine-ester hydrolase
Systematic name: \(N^5\)-acyl-L-ornithine-ester hydrolase
Comments: Hydrolyses the three ornithine ester bonds in fusarinine C. Also acts on \(N^5\)-dinitrophenyl-L-ornithine methyl ester.
References: [622]

EC 3.1.1.48

Accepted name: sinapine esterase
Reaction: sinapoylcholine + H\textsubscript{2}O = sinapate + choline
Other name(s): aromatic choline esterase
Systematic name: sinapoylcholine sinapohydrolase
References: [1839]

EC 3.1.1.49

Accepted name: wax-ester hydrolase
Reaction: a wax ester + H\textsubscript{2}O = a long-chain alcohol + a long-chain carboxylate
Other name(s): jojoba wax esterase; WEH
Systematic name: wax-ester acylhydrolase
Comments: Also acts on long-chain acylglycerol, but not diacyl- or triacylglycerols.
References: [1055, 1701]

EC 3.1.1.50

Accepted name: phorbol-diester hydrolase
Reaction: phorbol 12,13-dibutanoate + H\textsubscript{2}O = phorbol 13-butanoate + butanoate
Other name(s): diacylphorbate 12-hydrolase; diacylphorbate 12-hydrolase; phorbol-12,13-diester 12-ester hydrolase; PDEH
Systematic name: 12,13-diacylphorbate 12-acylhydrolase
Comments: Hydrolyses the 12-ester bond in a variety of 12,13-diacylphorbols (phorbol is a diterpenoid); this reaction inactivates the tumour promotor 12-\(O\)-tetradecanoylphorbol-13-acetate from croton oil.
References: [2314]
EC 3.1.1.52
Accepted name: phosphatidylinositol deacylase
Reaction: 1-phosphatidyl-D-myoinositol + H₂O = 1-acylglycerophosphoinositol + a carboxylate
Other name(s): phosphatidylinositol phospholipase A₂; phospholipase A₂
Systematic name: 1-phosphatidyl-D-myoinositol 2-acylhydrolase
References: [862, 861]

EC 3.1.1.53
Accepted name: sialate O-acetylerase
Reaction: N-acetyl-O-acetyleneuraminate + H₂O = N-acetyleneuraminate + acetate
Other name(s): N-acetyleneuraminate acetyltransferase; sialate 9(4)-O-acetylerase; sialidase
Systematic name: N-acetyl-O-acetyleneuraminate O-acetylhydrolase
Comments: Acts on free and glycosidically bound N-acetyl- or N-glycoloyl-neuraminic acid; acts mainly on the 4-O- and 9-O-acetyl groups. Also acts on some other O-acetyl esters, both cyclic and acyclic compounds, which are not sialic acids.
References: [779, 2315]

EC 3.1.1.54
Accepted name: acetoxybutynylbithiophene deacetylase
Reaction: 5-(4-acetoxybut-1-ynyl)-2,2'-bithiophene + H₂O = 5-(4-hydroxybut-1-ynyl)-2,2'-bithiophene + acetate
Other name(s): acetoxybutynylbithiophene esterase; 5-(4-acetoxy-1-butynyl)-2,2'-bithiophene:acetate esterase
Systematic name: 5-(4-acetoxybut-1-ynyl)-2,2'-bithiophene O-acetylhydrolase
Comments: The enzyme is highly specific.
References: [2456]

EC 3.1.1.55
Accepted name: acetylsalicylate deacetylase
Reaction: acetylsalicylate + H₂O = salicylate + acetate
Other name(s): aspirin esterase; aspirin esterase; acetylsalicylic acid esterase; aspirin hydrolase
Systematic name: acetylsalicylate O-acetylhydrolase
Comments: Not identical with EC 3.1.1.1 (carboxylesterase), EC 3.1.1.2 (arylesterase), EC 3.1.1.7 (acetylcholinesterase) or EC 3.1.1.8 (cholinesterase). The activity of the liver cytosol enzyme is highest with acetyl esters of aryl alcohols, and thioesters are also hydrolysed; the microsomal enzyme also hydrolysos some other negatively charged esters, with highest activity on esters of salicylate with long-chain alcohols.
References: [32, 1255, 2789]

EC 3.1.1.56
Accepted name: methylumbelliferyl-acetate deacetylase
Reaction: 4-methylumbelliferyl acetate + H₂O = 4-methylumbelliferone + acetate
Other name(s): esterase D
**Systematic name:** 4-methylumbelliferyl-acetate acylhydrolase  
**Comments:** Acts on short-chain acyl esters of 4-methylumbelliferone, but not on naphthyl, indoxyl or thiocholine esters.  
**References:** [1038]

[EC 3.1.1.56 created 1986]

**EC 3.1.1.57**  
**Accepted name:** 2-pyrone-4,6-dicarboxylate lactonase  
**Reaction:** 2-pyrone-4,6-dicarboxylate + H₂O = 4-carboxy-2-hydroxyhexa-2,4-dienedioate  
**Systematic name:** 2-pyrone-4,6-dicarboxylate lactonohydrolase  
**Comments:** The product isomerizes to 4-oxalmesaconate.  
**References:** [1234, 1581]

[EC 3.1.1.57 created 1986]

**EC 3.1.1.58**  
**Accepted name:** N-acetylgalactosaminoglycan deacetylase  
**Reaction:** N-acetyl-D-galactosaminoglycan + H₂O = D-galactosaminoglycan + acetate  
**Other name(s):** polysaccharide deacetylase; polysaccharide deacetylase; Vi-polysaccharide deacetylase; N-acetyl galactosaminoglycan deacetylase  
**Systematic name:** N-acetyl-D-galactosaminoglycan acetylhydrolase  
**References:** [1160]

[EC 3.1.1.58 created 1986]

**EC 3.1.1.59**  
**Accepted name:** juvenile-hormone esterase  
**Reaction:** methyl (2E,6E)-(10R,11S)-10,11-epoxy-3,7,11-trimethyltrideca-2,6-dienoate + H₂O = (2E,6E)-(10R,11S)-10,11-epoxy-3,7,11-trimethyltrideca-2,6-dienoate + methanol  
**Other name(s):** JH-esterase; juvenile hormone analog esterase; juvenile hormone carboxyesterase  
**Systematic name:** methyl-(2E,6E)-(10R,11S)-10,11-epoxy-3,7,11-trimethyltrideca-2,6-dienoate acylhydrolase  
**Comments:** Demethylates the insect juvenile hormones, JH₁ and JH₃, but does not hydrolyse the analogous ethyl or isopropyl esters.  
**References:** [498, 1675]

[EC 3.1.1.59 created 1989]

**EC 3.1.1.60**  
**Accepted name:** bis(2-ethylhexyl)phthalate esterase  
**Reaction:** bis(2-ethylhexyl)phthalate + H₂O = 2-ethylhexyl phthalate + 2-ethylhexan-1-ol  
**Other name(s):** DEHP esterase  
**Systematic name:** bis(2-ethylhexyl)phthalate acylhydrolase  
**Comments:** Also acts on 4-nitrophenyl esters, with optimum chain-length C₆ to C₈.  
**References:** [896]

[EC 3.1.1.60 created 1989]

**EC 3.1.1.61**  
**Accepted name:** protein-glutamate methylesterase  
**Reaction:** protein L-glutamate O₅-methyl ester + H₂O = protein L-glutamate + methanol
**Other name(s):** chemotaxis-specific methylesterase; methyl-accepting chemotaxis protein methyl-esterase; CheB methylesterase; methylesterase CheB; protein methyl-esterase; protein carboxyl methylesterase; PME; protein methylesterase; protein-L-glutamate-5-O-methyl-ester acylhydrolase

**Systematic name:** protein-L-glutamate-5-O-methyl-ester acylhydrolase

**Comments:** Hydrolyses the products of EC 2.1.1.77 (protein-L-isoaaspartate (d-aspartate) O-methyltransferase), EC 2.1.1.78 (isoorientin 3′-O-methyltransferase), EC 2.1.1.80 (protein-glutamate O-methyltransferase) and EC 2.1.1.100 (protein-S-isoprenylcysteine O-methyltransferase).

**References:** [772, 1222]

**[EC 3.1.1.61 created 1989, modified 2002]**

**3.1.1.62** Deleted entry. *N-acetyldiaminopimelate deacetylase. Now listed as EC 3.5.1.47, N-acetyldiaminopimelate deacetylase*

**[EC 3.1.1.62 created 1989, deleted 1992]**

**EC 3.1.1.63**

**Accepted name:** 11-cis-retinyl-palmitate hydrolase

**Reaction:** 11-cis-retinyl palmitate + H₂O = 11-cis-retinol + palmitate

**Other name(s):** 11-cis-retinol palmitate esterase; RPH

**Systematic name:** 11-cis-retinyl-palmitate acylhydrolase

**Comments:** Activated by bile salts.

**References:** [217, 218]

**[EC 3.1.1.63 created 1989]**

**EC 3.1.1.64**

**Accepted name:** all-trans-retinyl-palmitate hydrolase

**Reaction:** all-trans-retinyl palmitate + H₂O = all-trans-retinol + palmitate

**Systematic name:** all-trans-retinyl-palmitate acylhydrolase

**Comments:** Requires detergents for activity.

**References:** [217]

**[EC 3.1.1.64 created 1989]**

**EC 3.1.1.65**

**Accepted name:** L-rhamnono-1,4-lactonase

**Reaction:** L-rhamnono-1,4-lactone + H₂O = L-rhamnonate

**Other name(s):** L-rhammo-γ-lactonase; L-rhammono-γ-lactonase; L-rhamnonate dehydratase

**Systematic name:** L-rhamnono-1,4-lactone lactonohydrolase

**References:** [2112]

**[EC 3.1.1.65 created 1989]**

**EC 3.1.1.66**

**Accepted name:** 5-(3,4-diacetoxybut-1-ynyl)-2,2′-bithiophene deacetylase

**Reaction:** 5-(3,4-diacetoxybut-1-ynyl)-2,2′-bithiophene + H₂O = 5-(3-hydroxy-4-acetoxybut-1-ynyl)-2,2′-bithiophene + acetate

**Other name(s):** diacetoxybutylbithiophene acetate esterase; 3,4-diacetoxybutylbithiophene:4-acetate esterase

**Systematic name:** 5-(3,4-diacetoxybut-1-ynyl)-2,2′-bithiophene acetylhydrolase

**Comments:** A highly specific enzyme from *Tagetes patula*.

**References:** [1959]
**EC 3.1.1.66**  
**Accepted name:** fatty-acyl-ethyl-ester synthase  
**Reaction:** a long-chain-fatty-acyl ethyl ester + H₂O = a long-chain-fatty acid + ethanol  
**Other name(s):** FAEES  
**Systematic name:** long-chain-fatty-acyl-ethyl-ester acylhydrolase  
**Comments:** In the reverse reaction, forms ethyl esters from fatty acids and ethanol in the absence of coenzyme A or ATP. Best substrates are unsaturated octadecanoic acids; palmitate, stearate and arachidonate also act, but more slowly.  
**References:** [1689]  

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**EC 3.1.1.67**  
**Accepted name:** fatty-acyl-ethyl-ester synthase  
**Reaction:** a long-chain-fatty-acyl ethyl ester + H₂O = a long-chain-fatty acid + ethanol  
**Other name(s):** FAEES  
**Systematic name:** long-chain-fatty-acyl-ethyl-ester acylhydrolase  
**Comments:** In the reverse reaction, forms ethyl esters from fatty acids and ethanol in the absence of coenzyme A or ATP. Best substrates are unsaturated octadecanoic acids; palmitate, stearate and arachidonate also act, but more slowly.  
**References:** [1689]  

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**EC 3.1.1.68**  
**Accepted name:** xylo-1,4-lactonase  
**Reaction:** d-xylo-1,4-lactone + H₂O = d-xyxonate  
**Other name(s):** xylo-1,4-lactonase; xylonolactonase  
**Systematic name:** d-xylo-1,4-lactone lactonohydrolase  
**References:** [300]  

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**[3.1.1.69 Transferred entry. N-acetylglucosaminylphosphatidylinositol deacetylase. Now EC 3.5.1.89, N-acetylglucosaminylphosphatidylinositol deacetylase. Previously classified erroneously as an enzyme that hydrolysed an ester and not an amide]**  

**EC 3.1.1.69**  
**Accepted name:** cetraxate benzylesterase  
**Reaction:** cetraxate benzyl ester + H₂O = cetraxate + benzyl alcohol  
**Systematic name:** cetraxate-benzyl-ester benzylhydrolase  
**Comments:** Acts on a number of benzyl esters of substituted phenyl propanoates, and on the benzyl esters of phenylalanine and tyrosine.  
**References:** [1361]  

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**EC 3.1.1.70**  
**Accepted name:** cetraxate benzylesterase  
**Reaction:** cetraxate benzyl ester + H₂O = cetraxate + benzyl alcohol  
**Systematic name:** cetraxate-benzyl-ester benzylhydrolase  
**Comments:** Acts on a number of benzyl esters of substituted phenyl propanoates, and on the benzyl esters of phenylalanine and tyrosine.  
**References:** [1361]  

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**EC 3.1.1.71**  
**Accepted name:** acetylalkylglycerol acetylhydrolase  
**Reaction:** 2-acetyl-1-alkyl-sn-glycerol + H₂O = 1-alkyl-sn-glycerol + acetate  
**Other name(s):** alkylacylglcerol acetylhydrolase  
**Systematic name:** 2-acetyl-1-alkyl-sn-glycerol acetylhydrolase  
**Comments:** Hydrolysis of the acetyl group from the 1-alkyl-2-acetyl and 1-alkyl-3-acetyl substrates occurs at apparently identical rates. The enzyme from Erlich ascites cells is membrane-bound. It differs from lipoprotein lipase (EC 3.1.1.34) since 1,2-diacetyl-sn-glycerols are not substrates. It also differs from EC 3.1.1.47, 1-acetyl-2-alkyl-glycerophosphocholine esterase.  
**References:** [220]  

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**EC 3.1.1.72**  
**Accepted name:** acetylxylan esterase
Reaction: Deacetylation of xylans and xylo-oligosaccharides
Systematic name: acetylxylan esterase
Comments: Catalyses the hydrolysis of acetyl groups from polymeric xylan, acetylated xylose, acetylated glucose, α-naphthyl acetate, p-nitrophenyl acetate but not from triacylglycerol. Does not act on acetylated mannan or pectin.
References: [2451, 2014, 1564]

EC 3.1.1.72
Accepted name: feruloyl esterase
Reaction: feruloyl-polysaccharide + H₂O = ferulate + polysaccharide
Other name(s): ferulic acid esterase, hydroxycinnamoyl esterase, hemicellulase accessory enzymes; FAE-III, cinnamoyl ester hydrolase, FAEA, cinnAE, FAE-I, FAE-II
Systematic name: 4-hydroxy-3-methoxycinnamoyl-sugar hydrolase
Comments: Catalyses the hydrolysis of the 4-hydroxy-3-methoxycinnamoyl (feruloyl) group from an esterified sugar, which is usually arabinose in "natural" substrates. p-Nitrophenol acetate and methyl ferulate are poorer substrates. All microbial ferulate esterases are secreted into the culture medium. They are sometimes called hemicellulase accessory enzymes, since they help xylanases and pectinases to break down plant cell wall hemicellulose.
References: [669, 670, 1333, 533, 345]

EC 3.1.1.73
Accepted name: cutinase
Reaction: cutin + H₂O = cutin monomers
Systematic name: cutin hydrolase
Comments: Cutin, a polymeric structural component of plant cuticles, is a polymer of hydroxy fatty acids that are usually C₁₆ or C₁₈ and contain up to three hydroxy groups. The enzyme from several fungal sources also hydrolyses the p-nitrophenyl esters of hexadecanoic acid. It is however inactive towards several esters that are substrates for non-specific esterases.
References: [778, 2024, 2023]

EC 3.1.1.74
Accepted name: poly(3-hydroxybutyrate) depolymerase
Other name(s): PHB depolymerase; poly(3HB) depolymerase; poly[(R)-hydroxyalkanoic acid] depolymerase; poly(HA) depolymerase; poly(HA₆Cl) depolymerase; poly[(R)-3-hydroxybutyrate] hydrolase
Systematic name: poly[(R)-3-hydroxybutanoate] hydrolase
Comments: Reaction also occurs with esters of other short-chain-length (C₁-C₅) hydroxyalkanoic acids (HA). There are two types of polymers: native (intracellular) granules are amorphous and have an intact surface layer; denatured (extracellular) granules either have no surface layer or a damaged surface layer and are partially crystalline.
References: [1140, 776]

EC 3.1.1.75
Accepted name: poly(3-hydroxyoctanoate) depolymerase
Reaction: Hydrolyses the polyester polyoxycarbonyl[(R)-2-pentylethylene] to oligomers

Other name(s): PHO depolymerase, poly(3HO) depolymerase; poly[(R)-hydroxyalkanoic acid] depolymerase; poly(HA) depolymerase; poly[(R)-3-hydroxyoctanoate] hydrolase

Systematic name: polyoxycarbonyl[(R)-2-pentylethylene] hydrolase

Comments: The main product after prolonged incubation is the dimer [2243]. Besides hydrolysing polymers of 3-hydroxyoctanoic acid, the enzyme also hydrolyses other polymers derived from medium-chain-length (C₆-C₁₂) hydroxyalkanoic acids and copolymers of mixtures of these. It also hydrolyses p-nitrophenyl esters of fatty acids. Polymers of short-chain-length hydroxyalkanoic acids such as poly[(R)-3-hydroxybutanoic acid] and poly[(R)-3-hydroxypentanoic acid] are not hydrolysed.

References: [1140, 776, 2243]

[EC 3.1.1.76 created 2001, modified 2005]

EC 3.1.1.77

Accepted name: acyloxyacyl hydrolase

Reaction: 3-(acyloxy)acyl group of bacterial toxin = 3-hydroxyacyl group of bacterial toxin + a fatty acid

Comments: The substrate is lipid A on the reducing end of the toxic lipopolysaccharide (LPS) of Salmonella typhimurium and related organisms. It consists of diglucosamine, β-D-GlcN-(1→6)-D-GlcN, attached by glycosylation on O-6 of its non-reducing residue, phosphorylated on O-4 of this residue and on O-1 of its potentially reducing residue. Both residues carry 3-(acyloxy)acyl groups on N-2 and O-3. The enzyme from human leucocytes detoxifies the lipid by hydrolysing the secondary acyl groups from O-3 of the 3-hydroxyacyl groups on the disaccharide (LPS). It also possesses a wide range of phospholipase and acyltransferase activities [e.g. EC 3.1.1.4 (phospholipase A₂), EC 3.1.1.5 (lysophospholipase), EC 3.1.1.32 (phospholipase A₁) and EC 3.1.1.52 (phosphatidylinositol deacylase)], hydrolysing diacylglycerol and phosphatidyl compounds, but not triacylglycerols. It has a preference for saturated C₁₂-C₁₆ acyl groups.

References: [640, 905, 1734]

[EC 3.1.1.77 created 2001]

EC 3.1.1.78

Accepted name: polyneuridine-aldehyde esterase

Reaction: polyneuridine aldehyde + H₂O = 16-epivellosimine + CO₂ + methanol

Other name(s): polyneuridine aldehyde esterase; PNAE

Systematic name: polyneuridine aldehyde hydrolase (decarboxylating)

Comments: Following hydrolysis of this indole alkaloid ester the carboxylic acid decarboxylates spontaneously giving the sarpagan skeleton. The enzyme also acts on akuammidine aldehyde (the 16-epimer of polyneuridine aldehyde).

References: [1968, 1969, 560, 1598]

[EC 3.1.1.78 created 2002]

EC 3.1.1.79

Accepted name: hormone-sensitive lipase

Reaction: (1) diacylglycerol + H₂O = monoacylglycerol + a carboxylate
(2) triacylglycerol + H₂O = diacylglycerol + a carboxylate
(3) monoacylglycerol + H₂O = glycerol + a carboxylate

Other name(s): HSL

Systematic name: diacylglycerol acylhydrolase
Comments: This enzyme is a serine hydrolase. Compared with other lipases, hormone-sensitive lipase has a uniquely broad substrate specificity. It hydrolyses all acylglycerols (triacylglycerol, diacylglycerol and monoacylglycerol) [2,3,4] as well as cholesteryl esters [720, 1912], steroid fatty acid esters [1400], retinyl esters [2767] and \( p \)-nitrophenyl esters [1912, 2609]. It exhibits a preference for the 1- or 3-ester bond of its acylglycerol substrate compared with the 2-ester bond [2880]. The enzyme shows little preference for the fatty acids in the triacylglycerol, although there is some increase in activity with decreasing chain length. The enzyme activity is increased in response to hormones that elevate intracellular levels of cAMP.

References: [1028, 720, 2685, 1912, 1400, 2767, 2609, 2880]

[EC 3.1.1.79 created 2004]

EC 3.1.1.80
Accepted name: acetylajmaline esterase
Reaction: (1) 17-\( O \)-acetylajmaline + \( H_2O \) = ajmaline + acetate
(2) 17-\( O \)-acetylnorajmaline + \( H_2O \) = norajmaline + acetate
Other name(s): AAE; \( 2(R) \)-17-\( O \)-acetylajmalan:acylesterase; acetylajmalan esterase
Systematic name: 17-\( O \)-acetylajmaline \( O \)-acyethylhydrolase
Comments: This plant enzyme is responsible for the last stages in the biosynthesis of the indole alkaloid ajmaline. The enzyme is highly specific for the substrates 17-\( O \)-acetylajmaline and 17-\( O \)-acetylnorajmaline as the structurally related acetylated alkaloids vinorine, vomilenine, 1,2-dihydrovomilenine and 1,2-dihydroraucaffricine cannot act as substrates [2166]. This is a novel member of the GDSL family of serine esterases/lipases.

References: [2002, 2166]

[EC 3.1.1.80 created 2006]

EC 3.1.1.81
Accepted name: quorum-quenching \( N \)-acyl-homoserine lactonase
Reaction: an \( N \)-acyl-L-homoserine lactone + \( H_2O \) = an \( N \)-acyl-L-homoserine
Other name(s): acyl homoserine degrading enzyme; acyl-homoserine lactone acylase; AHL lactonase; AHL-degrading enzyme; AHL-inactivating enzyme; AHLase; AhID; AhIK; AiiA; AiiA lactonase; AiiA-like protein; AiiB; AiiC; AttM; delactonase; lactonase-like enzyme; \( N \)-acyl homoserine lactonase; \( N \)-acyl homoserine lactone hydrolase; \( N \)-acyl-homoserine lactone lactonohydrolase; quorum-quenching lactonase; quorum-quenching \( N \)-acyl homoserine lactone hydrolase
Systematic name: \( N \)-acyl-L-homoserine-lactone lactonohydrolase
Comments: Acyl-homoserine lactones (AHLs) are produced by a number of bacterial species and are used by them to regulate the expression of virulence genes in a process known as quorum-sensing. Each bacterial cell has a basal level of AHL and, once the population density reaches a critical level, it triggers AHL-signalling which, in turn, initiates the expression of particular virulence genes [567]. Plants or animals capable of degrading AHLs would have a therapeutic advantage in avoiding bacterial infection as they could prevent AHL-signalling and the expression of virulence genes in quorum-sensing bacteria [567]. \( N \)-(3-Oxohexanoyl)-L-homoserine lactone, \( N \)-(3-oxododecanoyl)-L-homoserine lactone, \( N \)-butanoyl-L-homoserine lactone and \( N \)-(3-oxooctanoyl)-L-homoserine lactone can act as substrates [567].

References: [2554, 566, 2736, 568, 567, 1406, 1940, 2638, 1262, 1484, 2857]

[EC 3.1.1.81 created 2007]

EC 3.1.1.82
Accepted name: pheophorbidase
Reaction: pheophorbide \( a \) + \( H_2O \) = pyropheophorbide \( a \) + methanol + \( CO_2 \) (overall reaction)
(1a) pheophorbide \( a \) + \( H_2O \) = \( C-13^2 \)-carboxylyopheophorbide \( a \) + methanol

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Other name(s): C-13\(^2\)-carboxypyropheophorbide \(a = \text{pyropheophorbide } a + \text{CO}_2\) (spontaneous)
Systematic name: phoephyorbide-\(a\) hydrolase

Comments: This enzyme forms part of the chlorophyll degradation pathway, and is found in higher plants and in algae. In higher plants it participates in de-greening processes such as fruit ripening, leaf senescence, and flowering. The enzyme exists in two forms: type 1 is induced by senescence whereas type 2 is constitutively expressed [2464, 2463]. The enzyme is highly specific for pheophorbide as substrate (with a preference for pheophorbide \(a\) over pheophorbide \(b\)) as other chlorophyll derivatives such as protochlorophyllide \(a\), pheophytin \(a\) and \(c\), chlorophyll \(a\) and \(b\), and chlorophyllide \(a\) cannot act as substrates [2463]. Another enzyme, called phoepborbide demethoxycarbonylase (PDC), produces pyropheophorbide \(a\) from pheophorbide \(a\) without forming an intermediate although the precise reaction is not yet known [2464].

References: [2464, 2463, 1042]

[EC 3.1.1.82 created 2007]

EC 3.1.1.83
Accepted name: monoterpene \(\epsilon\)-lactone hydrolase
Reaction: 
(1) isoprop(en)ylmethyloxepan-2-one + H\(_2\)O = 6-hydroxyisoprop(en)ylmethylhexanoate (general reaction)
(2) 4-isopropenyl-7-methyloxepan-2-one + H\(_2\)O = 6-hydroxy-3-isopropenilyheptanoate
(3) 7-isopropyl-4-methyloxepan-2-one + H\(_2\)O = 6-hydroxy-3,7-dimethyloctanoate

Other name(s): MLH
Systematic name: isoprop(en)ylmethyloxepan-2-one lactonohydrolase
Comments: The enzyme catalyses the ring opening of \(\epsilon\)-lactones which are formed during degradation of dihydrocarveol by the Gram-positive bacterium \textit{Rhodococcus erythropolis} DCL14. The enzyme also acts on ethyl caproate, indicating that it is an esterase with a preference for lactones (internal cyclic esters). The enzyme is not stereoselective.

References: [2671]

[EC 3.1.1.83 created 2008]

EC 3.1.1.84
Accepted name: cocaine esterase
Reaction: cocaine + H\(_2\)O = ecgonine methyl ester + benzoate
Other name(s): CocE; hCE2; hCE-2; human carboxylesterase 2
Systematic name: cocaine benzoylhydrolase
Comments: \textit{Rhodococcus} sp. strain MB1 and \textit{Pseudomonas maltophilia} strain MB11L can utilize cocaine as sole source of carbon and energy [265, 271].

References: [775, 265, 271, 1380, 1983]

[EC 3.1.1.84 created 2010]

EC 3.1.2 Thioester hydrolases

EC 3.1.2.1
Accepted name: acetyl-CoA hydrolase
Reaction: acetyl-CoA + H\(_2\)O = CoA + acetate
Other name(s): acetyl-CoA deacylase; acetyl-CoA acylase; acetyl coenzyme A hydrolase; acetyl coenzyme A deacylase; acetyl coenzyme A acylase; acetyl-CoA thiol esterase
Systematic name: acetyl-CoA hydrolase
References: [798]
EC 3.1.2.1
Accepted name: palmitoyl-CoA hydrolase
Reaction: palmitoyl-CoA + H₂O = CoA + palmitate
Other name(s): long-chain fatty-acyl-CoA hydrolase; palmitoyl coenzyme A hydrolase; palmitoyl thioesterase; palmitoyl coenzyme A hydrolase; palmitoyl-CoA deacylase; palmitoyl thioesterase; palmitoyl-CoA deacylase; fatty acyl thioesterase I; palmitoyl thioesterase I
Systematic name: palmitoyl-CoA hydrolase
Comments: Also hydrolyses CoA thioesters of other long-chain fatty acids.
References: [129, 174, 1682, 2404, 2838]

EC 3.1.2.2
Accepted name: palmitoyl-CoA hydrolase
Reaction: palmitoyl-CoA + H₂O = CoA + palmitate
Other name(s): long-chain fatty-acyl-CoA hydrolase; palmitoyl coenzyme A hydrolase; palmitoyl thioesterase; palmitoyl coenzyme A hydrolase; palmitoyl-CoA deacylase; palmitoyl thioesterase; palmitoyl-CoA deacylase; fatty acyl thioesterase I; palmitoyl thioesterase I
Systematic name: palmitoyl-CoA hydrolase
Comments: Also hydrolyses CoA thioesters of other long-chain fatty acids.
References: [129, 174, 1682, 2404, 2838]

EC 3.1.2.3
Accepted name: succinyl-CoA hydrolase
Reaction: succinyl-CoA + H₂O = CoA + succinate
Other name(s): succinyl-CoA acylase; succinyl coenzyme A hydrolase; succinyl coenzyme A deacylase
Systematic name: succinyl-CoA hydrolase
References: [798]

EC 3.1.2.4
Accepted name: 3-hydroxyisobutyryl-CoA hydrolase
Reaction: 3-hydroxy-2-methylpropanoyl-CoA + H₂O = CoA + 3-hydroxy-2-methylpropanoate
Other name(s): 3-hydroxyisobutyryl-CoA hydrolase; HIB CoA deacylase
Systematic name: 3-hydroxy-2-methylpropanoyl-CoA hydrolase
Comments: Also hydrolyses 3-hydroxypropanoyl-CoA.
References: [2095]

EC 3.1.2.5
Accepted name: hydroxymethylglutaryl-CoA hydrolase
Reaction: (S)-3-hydroxy-3-methylglutaryl-CoA + H₂O = CoA + 3-hydroxy-3-methylglutarate
Other name(s): β-hydroxy-β-methylglutaryl coenzyme A hydrolase; β-hydroxy-β-methylglutaryl coenzyme A deacylase; hydroxymethylglutaryl coenzyme A hydrolase; hydroxymethylglutaryl coenzyme A deacylase; 3-hydroxy-3-methylglutaryl-CoA hydrolase
Systematic name: (S)-3-hydroxy-3-methylglutaryl-CoA hydrolase
References: [510]

EC 3.1.2.6
Accepted name: hydroxyacylglutathione hydrolase
Reaction: S-(2-hydroxyacyl)glutathione + H₂O = glutathione + a 2-hydroxy carboxylate
Other name(s): glyoxalase II; S-2-hydroxyacylglutathione hydrolase; hydroxyacylglutathione hydrolase; acetoacetylglutathione hydrolase
Systematic name: S-(2-hydroxyacyl)glutathione hydrolase
Comments: Also hydrolyses S-acetoacetylglutathione, but more slowly.
References: [2038, 2645, 2646]
EC 3.1.2.7
Accepted name: glutathione thiolesterase
Reaction: S-acylglutathione + H₂O = glutathione + a carboxylate
Other name(s): citrilyl-glutathione thioesterlyase
Systematic name: S-acylglutathione hydrolase
References: [1249]

[EC 3.1.2.7 created 1961]

[3.1.2.8] **Deleted entry. S-acetoacylglutathione hydrolase. Now included with EC 3.1.2.6 hydroxyacylglutathione hydrolase**

[EC 3.1.2.8 created 1961, deleted 1978]

[3.1.2.9] **Deleted entry. S-acetoacylhydrolipoate hydrolase**

[EC 3.1.2.9 created 1961, deleted 1964]

EC 3.1.2.10
Accepted name: formyl-CoA hydrolase
Reaction: formyl-CoA + H₂O = CoA + formate
Other name(s): formyl coenzyme A hydrolase
Systematic name: formyl-CoA hydrolase
References: [2361]

[EC 3.1.2.10 created 1965]

EC 3.1.2.11
Accepted name: acetoacetyl-CoA hydrolase
Reaction: acetoacetyl-CoA + H₂O = CoA + acetoacetate
Other name(s): acetoacetyl coenzyme A hydrolase; acetoacetyl CoA deacylase; acetoacetyl coenzyme A deacylase
Systematic name: acetoacetyl-CoA hydrolase
References: [60, 584]

[EC 3.1.2.11 created 1972]

EC 3.1.2.12
Accepted name: S-formylglutathione hydrolase
Reaction: S-formylglutathione + H₂O = glutathione + formate
Systematic name: S-formylglutathione hydrolase
Comments: Also hydrolyses S-acetylglutathione, but more slowly.
References: [2645, 2648, 930]

[EC 3.1.2.12 created 1978]

EC 3.1.2.13
Accepted name: S-succinylglutathione hydrolase
Reaction: S-succinylglutathione + H₂O = glutathione + succinate
Systematic name: S-succinylglutathione hydrolase
References: [2645, 2647]

[EC 3.1.2.13 created 1978]
EC 3.1.2.14

Accepted name: oleoyl-[acyl-carrier-protein] hydrolase


Other name(s): acyl-[acyl-carrier-protein] hydrolase; acyl-ACP-hydrolase; acyl-acyl carrier protein hydrolase; oleoyl-ACP thioesterase; oleoyl-acyl carrier protein thioesterase; oleoyl-[acyl-carrier-protein] hydrolase

Systematic name: oleoyl-[acyl-carrier protein] hydrolase

Comments: Acts on acyl-carrier-protein thioesters of fatty acids from C₁₂ to C₁₈, but the derivative of oleic acid is hydrolysed much more rapidly than any other compound tested.

References: [1877, 2308]

[EC 3.1.2.14 created 1984]

EC 3.1.2.15

Accepted name: ubiquitin thiolesterase

Reaction: ubiquitin C-terminal thioester + H₂O = ubiquitin + a thiol

Other name(s): ubiquitin carboxy-terminal esterase; isopeptidase; isopeptidase T; ubiquitin C-terminal hydrolase; ubiquitin-C-terminal-thiolester hydrolase

Systematic name: ubiquitin-C-terminal-thioester hydrolase

Comments: Acts on esters formed between thiols such as dithiothreitol or glutathione and the C-terminal glycine residue of the polypeptide ubiquitin. Also acts on AMP-ubiquitin. May be the same as EC 3.4.19.12, ubiquitinyl hydrolase 1.

References: [2144]

[EC 3.1.2.15 created 1986]

EC 3.1.2.16

Accepted name: citrate-lyase deacetylase

Reaction: [citrate (pro-3S)-lyase](acetyl form) + 6 H₂O = [citrate (pro-3S)-lyase](thiol form) + 6 acetate

Other name(s): [citrate-(pro-3S)-lyase] thiolesterase; acetyl-S-(acyl-carrier protein) enzyme thioester hydrolase; citrate lyase deacetylase

Systematic name: [citrate-(pro-3S)-lyase](acetyl-form) hydrolase

Comments: In the proteobacterium Rubrivivax gelatinosus, this enzyme modulates the activity of EC 4.1.3.6, citrate (pro-3S)-lyase, by converting it from its active acetyl form into its inactive thiol form by removal of its acetyl groups [812]. The activity of citrate-lyase deacetylase is itself inhibited by L-glutamate [812].

References: [811, 812]

[EC 3.1.2.16 created 1989]

EC 3.1.2.17

Accepted name: (S)-methylmalonyl-CoA hydrolase

Reaction: (S)-methylmalonyl-CoA + H₂O = methylmalonate + CoA

Other name(s): d-methylmalonyl-coenzyme A hydrolase

Systematic name: (S)-methylmalonyl-CoA hydrolase

References: [1319]

[EC 3.1.2.17 created 1989]

EC 3.1.2.18

Accepted name: ADP-dependent short-chain-acyl-CoA hydrolase

Reaction: acyl-CoA + H₂O = CoA + a carboxylate

Other name(s): short-chain acyl coenzyme A hydrolase; propionyl coenzyme A hydrolase; propionyl-CoA hydrolase; propionyl-CoA thioesterase; short-chain acyl-CoA hydrolase; short-chain acyl-CoA thioesterase
Systematic name: ADP-dependent-short-chain-acyl-CoA hydrolase
Comments: Requires ADP; inhibited by NADH. Maximum activity is shown with propanoyl-CoA.
References: [29, 30]

[EC 3.1.2.18 created 1992]

EC 3.1.2.19
Accepted name: ADP-dependent medium-chain-acyl-CoA hydrolase
Reaction: acyl-CoA + H₂O = CoA + a carboxylate
Other name(s): medium-chain acyl coenzyme A hydrolase; medium-chain acyl-CoA hydrolase; medium-chain acyl-thioester hydrolase; medium-chain hydrolase; myristoyl-CoA thioesterase
Systematic name: ADP-dependent-medium-chain-acyl-CoA hydrolase
Comments: Requires ADP; inhibited by NADH. Maximum activity is shown with nonanoyl-CoA.
References: [29]

[EC 3.1.2.19 created 1992]

EC 3.1.2.20
Accepted name: acyl-CoA hydrolase
Reaction: acyl-CoA + H₂O = CoA + a carboxylate
Other name(s): acyl coenzyme A thioesterase; acyl-CoA thioesterase; acyl coenzyme A hydrolase; thioesterase B; thioesterase II; acyl-CoA thioesterase
Systematic name: acyl-CoA hydrolase
Comments: Broad specificity for medium- to long-chain acyl-CoA. Insensitive to NAD⁺ (cf. EC 3.1.2.19 ADP-dependent medium-chain-acyl-CoA hydrolase)
References: [30]

[EC 3.1.2.20 created 1992]

EC 3.1.2.21
Accepted name: dodecanoyl-[acyl-carrier-protein] hydrolase
Other name(s): lauryl-acyl-carrier-protein hydrolase; dodecanoyl-acyl-carrier-protein hydrolase; dodecyl-acyl-carrier protein hydrolase; dodecanoyl-[acyl-carrier protein] hydrolase; dodecanoyl-[acyl-carrier-protein] hydrolase
Systematic name: dodecanoyl-[acyl-carrier protein] hydrolase
References: [1999, 487]

[EC 3.1.2.21 created 1999]

EC 3.1.2.22
Accepted name: palmitoyl[protein] hydrolase
Reaction: palmitoyl[protein] + H₂O = palmitate + protein
Other name(s): palmitoyl-protein thioesterase; palmitoyl-(protein) hydrolase
Systematic name: palmitoyl[protein] hydrolase
Comments: Specific for long-chain thioesters of fatty acids. Hydrolyses fatty acids from S-acylated cysteine residues in proteins, palmitoyl cysteine and palmitoyl-CoA.
References: [328, 2256, 2690]

[EC 3.1.2.22 created 1999]
EC 3.1.2.23

Accepted name: 4-hydroxybenzoyl-CoA thioesterase
Reaction: \(4\text{-hydroxybenzoyl-CoA} + \text{H}_2\text{O} = 4\text{-hydroxybenzoate} + \text{CoA}\)
Systematic name: 4-hydroxybenzoyl-CoA hydrolase
Comments: This enzyme is part of the bacterial 2,4-dichlorobenzoate degradation pathway.
References: [359, 595]

[EC 3.1.2.23 created 1999]

[3.1.2.24 Transferred entry. 2-(2-hydroxyphenyl)benzenesulfinate hydrolase. Now EC 3.13.1.3, 2′-hydroxybiphenyl-2-sulfinate desulfinase. The enzyme was incorrectly classified as a thioester hydrolase when the bond broken is a C-S bond, which is not an ester]

[EC 3.1.2.24 created 2000, deleted 2005]

EC 3.1.2.25

Accepted name: phenylacetyl-CoA hydrolase
Reaction: phenylglyoxylyl-CoA + \text{H}_2\text{O} = \text{phenylglyoxylate} + \text{CoA}
Systematic name: phenylglyoxylyl-CoA hydrolase
Comments: This is the second step in the conversion of phenylacetyl-CoA to phenylglyoxylate, the first step being carried out by EC 1.17.5.1, phenylacetyl-CoA dehydrogenase.
References: [2103, 2252]

[EC 3.1.2.25 created 2004]

EC 3.1.2.26

Accepted name: bile-acid-CoA hydrolase
Reaction: deoxycholoyl-CoA + \text{H}_2\text{O} = \text{CoA} + \text{deoxycholate}
Systematic name: deoxycholoyl-CoA hydrolase
Comments: Choloyl-CoA, 3-dehydrocholoyl-CoA and chenodeoxycholoyl-CoA can also act as substrates, but acetyl-CoA, isovaleryl-CoA, palmitoyl-CoA and phenylacetyl-CoA cannot.
References: [2878]

[EC 3.1.2.26 created 2005]

EC 3.1.2.27

Accepted name: choloyl-CoA hydrolase
Reaction: choloyl-CoA + \text{H}_2\text{O} = \text{cholate} + \text{CoA}
Other name(s): PTE-2 (ambiguous); choloyl-coenzyme A thioesterase; chenodeoxycholoyl-coenzyme A thioesterase; peroxisomal acyl-CoA thioesterase 2
Systematic name: choloyl-CoA hydrolase
Comments: Also acts on chenodeoxycholoyl-CoA and to a lesser extent on short- and medium- to long-chain acyl-CoAs, and other substrates, including trihydroxycoprostanoyl-CoA, hydroxymethylglutaryl-CoA and branched chain acyl-CoAs, all of which are present in peroxisomes. The enzyme is strongly inhibited by CoA and may be involved in controlling CoA levels in the peroxisome [1060].
References: [1060, 2378, 2167]

[EC 3.1.2.27 created 2005]

EC 3.1.3 Phosphoric-monoester hydrolases

EC 3.1.3.1

Accepted name: alkaline phosphatase
Reaction: a phosphate monoester + $\text{H}_2\text{O} = \text{an alcohol} + \text{phosphate}$

Other name(s): alkaline phosphomonoesterase; phosphomonoesterase; glycerophosphatase; alkaline phosphohydrolase; alkaline phenyl phosphatase; orthophosphoric-monoester phosphohydrolase (alkaline optimum)

Systematic name: phosphate-monoester phosphohydrolase (alkaline optimum)

Comments: Wide specificity. Also catalyses transphosphorylations. The human placental enzyme is a zinc protein. Some enzymes hydrolyse diphosphate (cf. EC 3.6.1.1 inorganic diphosphatase)

References: [632, 928, 1542, 1718, 2411]

EC 3.1.3.2

Accepted name: acid phosphatase

Reaction: a phosphate monoester + $\text{H}_2\text{O} = \text{an alcohol} + \text{phosphate}$

Other name(s): acid phosphomonoesterase; phosphomonoesterase; glycerophosphatase; acid monophosphatase; acid phosphohydrolase; acid phosphomonoester hydrolase; uteroferrin; acid nucleoside diphosphate phosphatase; orthophosphoric-monoester phosphohydrolase (acid optimum)

Systematic name: phosphate-monoester phosphohydrolase (acid optimum)

Comments: Wide specificity. Also catalyses transphosphorylations.

References: [1167, 1352, 2604]

EC 3.1.3.3

Accepted name: phosphoserine phosphatase

Reaction: $\text{O}-\text{phospho-L(}\text{or D})\text{-serine} + \text{H}_2\text{O} = \text{L(}\text{or D})\text{-serine} + \text{phosphate}$

Systematic name: $\text{O}-\text{phosphoserine phosphohydrolase}$

References: [243, 315, 1796]

EC 3.1.3.4

Accepted name: phosphatidate phosphatase

Reaction: a 1,2-diacylglycerol 3-phosphate + $\text{H}_2\text{O} = \text{a} \ 1,2\text{-diacyl-} sn\text{-glycerol} + \text{phosphate}$

Other name(s): phosphatic acid phosphatase; acid phosphatidyl phosphatase; phosphatic acid phosphohydrolase; PAP, Lipin

Systematic name: diacylglycerol-3-phosphate phosphohydrolase

Comments: This enzyme catalyses the $\text{Mg}^{2+}$-dependent dephosphorylation of a 1,2-diacylglycerol-3-phosphate, yielding a 1,2-diacyl- $ sn$-glycerol (DAG), the substrate for $de novo$ lipid synthesis via the Kennedy pathway and for the synthesis of triacylglycerol. In lipid signaling, the enzyme generates a pool of DAG to be used for protein kinase C activation. The mammalian enzymes are known as lipins.

References: [2369, 340]

EC 3.1.3.5

Accepted name: 5'-nucleotidase

Reaction: a 5'-ribonucleotide + $\text{H}_2\text{O} = \text{a} \ 5'$-ribonucleoside + phosphate

Other name(s): uridine 5'-nucleotidase; 5'-adenylic phosphatase; adenosine 5'-phosphatase; AMP phosphatase; adenosine monophosphatase; 5'-mononucleotidase; AMPase; UMPase; snake venom 5'-nucleotidase; thimidine monophosphate nucleotidase; 5'-AMPase; 5'-AMP nucleotidase; AMP phosphohydrolase; IMP 5'-nucleotidase

Systematic name: 5'-ribonucleotide phosphohydrolase

Comments: Wide specificity for 5'-nucleotides.

References: [887, 988, 2270]
[EC 3.1.3.5 created 1961]

EC 3.1.3.6

Accepted name: 3′-nucleotidase

Reaction: a 3′-ribonucleotide + H₂O = a ribonucleoside + phosphate

Other name(s): 3′-mononucleotidase; 3′-phosphatase; 3′-ribonucleotidase

Systematic name: 3′-ribonucleotide phosphohydrolase

Comments: Wide specificity for 3′-nucleotides.

References: [2316]

[EC 3.1.3.6 created 1961]

EC 3.1.3.7

Accepted name: 3′(2′),5′-bisphosphate nucleotidase

Reaction: adenosine 3′,5′-bisphosphate + H₂O = adenosine 5′-phosphate + phosphate

Other name(s): phosphoadenylate 3′-nucleotidase; 3′-phosphoadenyllylsulfate 3′-phosphatase; phosphoadenylate 3′-nucleotidase; 3′(2′),5′-bisphosphonucleoside 3′(2′)-phosphohydrolase

Systematic name: adenosine-3′(2′),5′-bisphosphate 3′(2′)-phosphohydrolase

Comments: Also acts on 3′-phosphoadenylyl sulfate, and on the corresponding 2′-phosphates.

References: [295, 663, 2051, 2601]

[EC 3.1.3.7 created 1961]

EC 3.1.3.8

Accepted name: 3-phytase

Reaction: myo-inositol hexakisphosphate + H₂O = 1D-myo-inositol 1,2,4,5,6-pentakisphosphate + phosphate

Other name(s): 1-phytase; phytase; phytate 1-phosphatase; phytate 6-phosphatase

Systematic name: myo-inositol-hexakisphosphate 3-phosphohydrolase

References: [441, 1149, 1095, 442]

[EC 3.1.3.8 created 1961, modified 1976, modified 2002]

EC 3.1.3.9

Accepted name: glucose-6-phosphatase

Reaction: D-glucose 6-phosphate + H₂O = D-glucose + phosphate

Other name(s): glucose 6-phosphate phosphatase

Systematic name: D-glucose-6-phosphate phosphohydrolase

Comments: Wide distribution in animal tissues. Also catalyses potent transphosphorylations from carbamoyl phosphate, hexose phosphates, diphosphate, phosphoenolpyruvate and nucleoside di- and triphosphates, to D-glucose, D-mannose, 3-methyl-D-glucose or 2-deoxy-D-glucose [cf. EC 2.7.1.62 (phosphoramidate—hexose phosphotransferase), EC 2.7.1.79 (diphosphate—glycerol phosphotransferase) and EC 3.9.1.1 (phosphoamidase)].

References: [47, 419, 1827, 1828]

[EC 3.1.3.9 created 1961]

EC 3.1.3.10

Accepted name: glucose-1-phosphatase

Reaction: α-D-glucose 1-phosphate + H₂O = α-D-glucose + phosphate

Systematic name: α-D-glucose-1-phosphate phosphohydrolase

Comments: Also acts, more slowly, on D-galactose 1-phosphate.

References: [671, 2627]
EC 3.1.3.11

**Accepted name:** fructose-bisphosphatase  
**Reaction:** \( \text{D-fructose 1,6-bisphosphate} + \text{H}_2\text{O} = \text{D-fructose 6-phosphate} + \text{phosphate} \)  
**Other name(s):** hexose diphosphatase; FBPase; fructose 1,6-diphosphatase; fructose 1,6-diphosphatase phosphatase; D-fructose 1,6-diphosphatase; fructose 1,6-bisphosphatase; fructose diphosphatase; fructose diphosphate phosphatase; fructose bisphosphate phosphatase; fructose 1,6-bisphosphate 1-phosphatase; fructose 1,6-bisphosphate phosphatase; hexose bisphosphatase; D-fructose-1,6-bisphosphate phosphatase  
**Systematic name:** \( \text{D-fructose-1,6-bisphosphate 1-phosphohydrolase} \)  
**Comments:** The animal enzyme also acts on sedoheptulose 1,7-bisphosphate.  
**References:** [616, 848, 1691, 2004]  

[EC 3.1.3.11 created 1961, modified 1976]

EC 3.1.3.12

**Accepted name:** trehalose-phosphatase  
**Reaction:** \( \alpha_\alpha\text{-trehalose 6-phosphate} + \text{H}_2\text{O} = \alpha_\alpha\text{-trehalose} + \text{phosphate} \)  
**Other name(s):** trehalose 6-phosphatase; trehalose 6-phosphate phosphatase; trehalose-6-phosphate phosphohydrolase  
**Systematic name:** \( \alpha_\alpha\text{-trehalose-6-phosphate phosphohydrolase} \)  
**References:** [319, 334]  

[EC 3.1.3.12 created 1961]

EC 3.1.3.13

**Accepted name:** bisphosphoglycerate phosphatase  
**Reaction:** \( 2,3\text{-bisphospho-}D\text{-glycerate} + \text{H}_2\text{O} = 3\text{-phospho-}D\text{-glycerate} + \text{phosphate} \)  
**Other name(s):** 2,3-diphosphoglycerate phosphatase; diphosphoglycerate phosphatase; 2,3-diphosphoglyceric acid phosphatase; 2,3-bisphosphoglycerate phosphatase; glycerate-2,3-diphosphate phosphatase  
**Systematic name:** \( 2,3\text{-bisphospho-}D\text{-glycerate 2-phosphohydrolase} \)  
**References:** [1166, 2061]  

[EC 3.1.3.13 created 1961]

EC 3.1.3.14

**Accepted name:** methylphosphothioglycerate phosphatase  
**Reaction:** \( S\text{-methyl-3-phospho-1-thio-}D\text{-glycerate} + \text{H}_2\text{O} = S\text{-methyl-1-thio-}D\text{-glycerate} + \text{phosphate} \)  
**Other name(s):** methylthiophosphoglycerate phosphatase  
**Systematic name:** \( S\text{-methyl-3-phospho-1-thio-}D\text{-glycerate phosphohydrolase} \)  
**References:** [207]  

[EC 3.1.3.14 created 1961]

EC 3.1.3.15

**Accepted name:** histidinol-phosphatase  
**Reaction:** \( \text{L-histidinol phosphate} + \text{H}_2\text{O} = \text{L-histidinol} + \text{phosphate} \)  
**Other name(s):** histidinol phosphate phosphatase; L-histidinol phosphate phosphatase; histidinolphosphate phosphatase; HPpase; histidinolphosphatase  
**Systematic name:** \( \text{L-histidinol-phosphate phosphohydrolase} \)  
**References:** [44]  

[EC 3.1.3.15 created 1961]
EC 3.1.3.16
Accepted name: phosphoprotein phosphatase
Reaction: a phosphoprotein + H₂O = a protein + phosphate
Other name(s): protein phosphatase-1; protein phosphatase-2A; protein phosphatase-2B; protein phosphatase-2C; protein D phosphatase; phosphospectrin phosphatase; casein phosphatase; *Aspergillus awamori* acid protein phosphatase; calcineurin; phosphatase 2A; phosphatase 2B; phosphatase II; phosphatase IB; phosphatase C-II; polycation modulated (PCM-) phosphatase; phosphopyruvate dehydrogenase phosphatase; phosphatase SP; branched-chain α-keto acid dehydrogenase phosphatase; BCKDH phosphatase; 3-hydroxy 3-methylglutaryl coenzymeA reductase phosphatase; HMG-CoA reductase phosphatase; phosphatase H-II; phosphatase III; phosphatase I; protein phosphatase; phosphatase IV
Systematic name: phosphoprotein phosphohydrolase
Comments: A group of enzymes removing the serine- or threonine-bound phosphate group from a wide range of phosphoproteins, including a number of enzymes that have been phosphorylated under the action of a kinase (cf. EC 3.1.3.48 protein-tyrosine-phosphatase). The spleen enzyme also acts on phenolic phosphates and phosphamides (cf. EC 3.9.1.1 phosphomimidase)
References: [531, 1090, 2450, 2582]

[EC 3.1.3.16 created 1961, modified 1989]

EC 3.1.3.17
Accepted name: [phosphorylase] phosphatase
Reaction: [phosphorylase a] + 4 H₂O = 2 [phosphorylase b] + 4 phosphate
Other name(s): PR-enzyme; phosphorylase a phosphatase; glycogen phosphorylase phosphatase; protein phosphatase C; type 1 protein phosphatase
Systematic name: [phosphorylase a] phosphohydrolase
References: [256, 858, 2048]

[EC 3.1.3.17 created 1961]

EC 3.1.3.18
Accepted name: phosphoglycolate phosphatase
Reaction: 2-phosphoglycolate + H₂O = glycolate + phosphate
Other name(s): phosphoglycolate hydrolase; 2-phosphoglycolate phosphatase; P-glycolate phosphatase; phosphoglycolate phosphatase
Systematic name: 2-phosphoglycolate phosphohydrolase
References: [399]

[EC 3.1.3.18 created 1965]

EC 3.1.3.19
Accepted name: glycerol-2-phosphatase
Reaction: glycerol 2-phosphate + H₂O = glycerol + phosphate
Other name(s): β-glycerophosphatase; β-glycerophosphate phosphatase; 2-glycerophosphatase
Systematic name: glycerol-2-phosphate phosphohydrolase
References: [2250, 2604]

[EC 3.1.3.19 created 1965]

EC 3.1.3.20
Accepted name: phosphoglycerate phosphatase
Reaction: D-glycerate 2-phosphate + H₂O = D-glycerate + phosphate
Other name(s): D-2-phosphoglycerate phosphatase; glycerophosphate phosphatase
Systematic name: D-glycerate-2-phosphate phosphohydrolase
References: [658]
EC 3.1.3.21
Accepted name: glycerol-1-phosphatase
Reaction: glycerol 1-phosphate + H₂O = glycerol + phosphate
Other name(s): α-glycerophosphatase; α-glycerol phosphatase; glycerol 3-phosphatase; glycerol-3-phosphate phosphatase; glycerol 3-phosphate phosphohydrolase
Systematic name: glycerol-1-phosphate phosphohydrolase
Comments: The *Dunaliella* enzyme acts more rapidly on sn-glycerol 1-phosphate than on the 3-phosphate. The enzyme from yeast also acts on propane-1,2-diol 1-phosphate, but not on a variety of other phosphate esters.
References: [2455]

EC 3.1.3.22
Accepted name: mannitol-1-phosphatase
Reaction: D-mannitol 1-phosphate + H₂O = D-mannitol + phosphate
Other name(s): mannitol-1-phosphate phosphatase
Systematic name: D-mannitol-1-phosphate phosphohydrolase
References: [2163, 2842]

EC 3.1.3.23
Accepted name: sugar-phosphatase
Reaction: sugar phosphate + H₂O = sugar + phosphate
Systematic name: sugar-phosphate phosphohydrolase
Comments: Has a wide specificity, acting on aldohexose 1-phosphates, ketohexose 1-phosphates, aldohexose 6-phosphates, ketohexose 6-phosphates, both phosphate ester bonds of fructose 1,6-bisphosphate, phosphoric esters of disaccharides, and on pentose and triose phosphates, but at a slower rate.
References: [1412]

EC 3.1.3.24
Accepted name: sucrose-phosphate phosphatase
Reaction: sucrose 6F-phosphate + H₂O = sucrose + phosphate
Other name(s): sucrose 6-phosphate hydrolase; sucrose-phosphate hydrolase; sucrose-phosphate phosphohydrolase; sucrose-6-phosphatase (incorrect); sucrose-phosphatase (incorrect); sucrose-6-phosphate phosphatase; SPP
Systematic name: sucrose-6F-phosphate phosphohydrolase
Comments: Requires Mg²⁺ for maximal activity [1511]. This is the final step in the sucrose-biosynthesis pathway. The enzyme is highly specific for sucrose 6-phosphate, with fructose 6-phosphate unable to act as a substrate [1511]. Belongs in the haloacid dehydrogenase (HAD) superfamily. The F of sucrose 6F-phosphate is used to indicate that the fructose residue of sucrose carries the substituent.
References: [955, 1511, 1512, 685]

EC 3.1.3.25
Accepted name: inositol-phosphate phosphatase
Reaction: \(\textit{myo}\)-inositol phosphate + \(H_2O\) \(\rightarrow\) \(\textit{myo}\)-inositol + phosphate

Other name(s): \(\textit{myo}\)-inositol-1(or 4)-monophosphatase; inositol 1-phosphatase; \(\textit{l}\)-\(\textit{myo}\)-inositol-1-phosphate phosphatase; \(\textit{myo}\)-inositol 1-phosphate phosphatase; inositol monophosphate phosphatase; inositol-1(or 4)-monophosphatase; \(\textit{myo}\)-inositol-1(or 4)-phosphate phosphohydrolase; \(\textit{myo}\)-inositol monophosphatase; \(\textit{myo}\)-inositol-1-phosphatase

Systematic name: \(\textit{myo}\)-inositol-phosphate phosphohydrolase

Comments: Acts on five of the six isomers of \(\textit{myo}\)-inositol phosphate, all except \(\textit{myo}\)-inositol 2-phosphate, but does not act on \(\textit{myo}\)-inositol bearing more than one phosphate group. It also acts on adenosine 2'-phosphate (but not the 3'- or 5'- phosphates), sn-glycerol 3-phosphate and glycerol 2-phosphate. Two isoforms are known [2894].

References: [615, 792, 909, 2894, 2825, 12]


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**EC 3.1.3.26**

Accepted name: 4-phytase

Reaction: \(\textit{myo}\)-inositol hexakisphosphate + \(H_2O\) \(\rightarrow\) 1D-\(\textit{myo}\)-inositol 1,2,3,5,6-pentakisphosphate + phosphate

Other name(s): 6-phytase (name based on 1L-numbering system and not 1D-numbering); phytase; phytate 6-phosphatase; \(\textit{myo}\)-inositol-hexakisphosphate 6-phosphohydrolase (name based on 1L-numbering system and not 1D-numbering)

Systematic name: \(\textit{myo}\)-inositol-hexakisphosphate 4-phosphohydrolase

References: [1149, 2577, 1460, 442]

[EC 3.1.3.26 created 1972, modified 1976, modified 2002]

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**EC 3.1.3.27**

Accepted name: phosphatidylglycerophosphatase

Reaction: phosphatidylglycerophosphate + \(H_2O\) \(\rightarrow\) phosphatidylglycerol + phosphate

Other name(s): phosphatidylglycerophosphate phosphatase; PGP phosphatase

Systematic name: phosphatidylglycerophosphate phosphohydrolase

References: [363]

[EC 3.1.3.27 created 1972]

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**EC 3.1.3.28**

Accepted name: ADP-phosphoglycerate phosphatase

Reaction: 3-(ADP)-2-phosphoglycerate + \(H_2O\) \(\rightarrow\) 3-(ADP)-glycerate + phosphate

Other name(s): adenosine diphosphate phosphoglycerate phosphatase

Systematic name: 3-(ADP)-2-phosphoglycerate phosphohydrolase

Comments: Also acts on 2,3-bisphosphoglycerate.

References: [2905]

[EC 3.1.3.28 created 1972]

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**EC 3.1.3.29**

Accepted name: N-acylneuraminate-9-phosphatase

Reaction: N-acylneuraminate 9-phosphate + \(H_2O\) \(\rightarrow\) N-acylneuraminate + phosphate

Other name(s): acylneuraminate 9-phosphatase; N-acylneuraminic acid 9-phosphate phosphatase; N-acylneuraminic (sialic) acid 9-phosphatase

Systematic name: N-acylneuraminate-9-phosphate phosphohydrolase

References: [1165]

[EC 3.1.3.29 created 1972]

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3.1.3.30  Deleted entry. 3′-phosphoadenylylsulfate 3′-phosphatase. Now included with EC 3.1.3.31 nucleotidase

[EC 3.1.3.30 created 1972, deleted 1992]

EC 3.1.3.31
Accepted name: nucleotidase
Reaction: a nucleotide + H₂O = a nucleoside + phosphate
Other name(s): nucleotide phosphatase; nucleotide-specific phosphatase; NSP I; NSP II; deoxyribonucleoside-activated nucleotidase (DAN); deoxyinosine-activated nucleotidase (DIAN); acid nucleotidase
Systematic name: nucleotide phosphohydrolase
Comments: A wide specificity for 2′, 3′- and 5′-nucleotides; also hydrolyses glycerol phosphate and 4-nitrophenyl phosphate.
References: [69]

[EC 3.1.3.31 created 1972 (EC 3.1.3.30 created 1972, incorporated 1992)]

EC 3.1.3.32
Accepted name: polynucleotide 3′-phosphatase
Reaction: a 3′-phosphopolynucleotide + H₂O = a polynucleotide + phosphate
Other name(s): 2′(3′)-polynucleotidase; DNA 3′-phosphatase; deoxyribonucleate 3′-phosphatase; 5′-polynucleotidekinase 3′-phosphatase
Systematic name: polynucleotide 3′-phosphohydrolase
Comments: Also hydrolyses nucleoside 2′-, 3′- and 5′-monophosphates, but only 2′- and 3′-phosphopolynucleotides.
References: [160]

[EC 3.1.3.32 created 1972]

EC 3.1.3.33
Accepted name: polynucleotide 5′-phosphatase
Reaction: a 5′-phosphopolynucleotide + H₂O = a polynucleotide + phosphate
Other name(s): 5′-polynucleotidase
Systematic name: polynucleotide 5′-phosphohydrolase
Comments: Does not act on nucleoside monophosphates. Induced in Escherichia coli by T-even phages.
References: [160]

[EC 3.1.3.33 created 1972]

EC 3.1.3.34
Accepted name: deoxynucleotide 3′-phosphatase
Reaction: a deoxynucleoside 3′-phosphate + H₂O = a deoxynucleoside + phosphate
Other name(s): 3′-deoxynucleotidase; 3′-deoxyribonucleotidase
Systematic name: deoxyribonucleotide 3′-phosphohydrolase
Comments: Also catalyses the selective removal of 3′-phosphate groups from DNA and oligodeoxynucleotides. Induced in Escherichia coli by T-even phages.
References: [160]

[EC 3.1.3.34 created 1972]

EC 3.1.3.35
Accepted name: thymidylate 5′-phosphatase
Reaction: thymidylate + H₂O = thymidine + phosphate

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Other name(s): thymidylate 5′-nucleotidase; deoxythymidylate 5′-nucleotidase; thymidylate nucleotidase; deoxythymidylic 5′-nucleotidase; deoxythymidylate phosphohydrolase; dTMPase

Systematic name: thymidylate 5′-phosphohydrolase

Comments: Acts on 5-methyl-DCMP and on TMP, but more slowly than on dTMP.

References: [59]

[EC 3.1.3.35 created 1972]

EC 3.1.3.36

Accepted name: phosphoinositide 5-phosphatase

Reaction: 1-phosphatidyl-1D-myoinositol 4,5-bisphosphate + H_2O = 1-phosphatidyl-1D-myoinositol 4-phosphate + phosphate

Other name(s): type II inositol polyphosphate 5-phosphatase; triphosphoinositide phosphatase; IP_3 phosphatase; PtdIns(4,5)P_2 phosphatase; triphosphoinositide phosphomonoesterase; diphosphoinositide phosphatase; inositol 1,4,5-triphosphate 5-phosphomonoesterase; inositol triphosphate 5-phosphomonoesterase; phosphatidylinositolinositol-5-bisphosphatase; phosphatidylinositol-4,5-bisphosphate phosphatase; phosphatidylinositolinositol-4,5-bisphosphate phosphatase; polyphosphoinositide lipid 5-phosphatase; phosphatidylinositol-5-bisphosphate phosphatase

Systematic name: phosphatidylinositol-5-bisphosphate 4-phosphohydrolase

Comments: These enzymes can also remove the 5-phosphate from Ins(1,4,5)P_3 and/or Ins(1,3,4,5)P_4. They are a diverse family of enzymes, with differing abilities to catalyse two or more of the four reactions listed. They are thought to use inositol lipids rather than inositol phosphates as substrates in vivo. All of them can use either or both of PtdIns(4,5)P_2 and PtdIns(3,4,5)P_3 as substrates; this is the main property that distinguishes them from EC 3.1.3.56, inositol-polypolyphosphate 5-phosphatase.

References: [496, 2119, 2825]

[EC 3.1.3.36 created 1972, modified 2002]

EC 3.1.3.37

Accepted name: sedoheptulose-bisphosphatase

Reaction: sedoheptulose 1,7-bisphosphate + H_2O = sedoheptulose 7-phosphate + phosphate

Other name(s): SBPase; sedoheptulose 1,7-diphosphate phosphatase; sedoheptulose 1,7-diphosphatase; sedoheptulose diphosphatase; sedoheptulose bisphosphatase; sedoheptulose 1,7-bisphosphatase

Systematic name: sedoheptulose-1,7-bisphosphate 1-phosphohydrolase

References: [2039, 2593]

[EC 3.1.3.37 created 1976]

EC 3.1.3.38

Accepted name: 3-phosphoglycerate phosphatase

Reaction: D-glycerate 3-phosphate + H_2O = D-glycerate + phosphate

Other name(s): D-3-Phosphoglycerate phosphatase; 3-PGA phosphatase

Systematic name: D-glycerate-3-phosphate phosphohydrolase

Comments: Wide specificity, but 3-phosphoglycerate is the best substrate.

References: [2055]

[EC 3.1.3.38 created 1976]

EC 3.1.3.39

Accepted name: streptomycin-6-phosphatase

Reaction: streptomycin 6-phosphate + H_2O = streptomycin + phosphate

Other name(s): streptomycin 6-phosphate phosphatase; streptomycin 6-phosphate phosphohydrolase; streptomycin-6-P phosphohydrolase

[EC 3.1.3.39 created 1977]
Systematic name: streptomycin-6-phosphate phosphohydrolase
Comments: Also acts on dihydrostreptomycin 3’α,6-bisphosphate and streptidine 6-phosphate.
References: [2722, 2723]

[EC 3.1.3.39 created 1976]

EC 3.1.3.40
Accepted name: guanidinodeoxy-scyllo-inositol-4-phosphatase
Reaction: 1-guanidino-1-deoxy-scyllo-inositol 4-phosphate + H2O = 1-guanidino-1-deoxy-scyllo-inositol + phosphate
Other name(s): 1-guanidino-scyllo-inositol 4-phosphatase; 1-guanidino-1-deoxy-scyllo-inositol-4-P phosphohydrolase
Systematic name: 1-guanidino-1-deoxy-scyllo-inositol-4-phosphate 4-phosphohydrolase
Comments:
References: [2723]

[EC 3.1.3.40 created 1976]

EC 3.1.3.41
Accepted name: 4-nitrophenylphosphatase
Reaction: 4-nitrophenyl phosphate + H2O = 4-nitrophenol + phosphate
Other name(s): nitrophenyl phosphatase; p-nitrophenylphosphatase; para-nitrophenyl phosphatase; K-pNPPase; NPase; PNPPase; Ecto-p-nitrophenyl phosphatase; p-nitrophenylphosphate phosphohydrolase
Systematic name: 4-nitrophenolphosphate phosphohydrolase
Comments: A number of other substances, including phenyl phosphate, 4-nitrophenyl sulfate, acetyl phosphate and glycerol phosphate, are not substrates.
References: [80, 81]

[EC 3.1.3.41 created 1976]

EC 3.1.3.42
Accepted name: [glycogen-synthase-D] phosphatase
Other name(s): uridine diphosphoglucose-glycogen glucosyltransferase phosphatase; UDP-glycogen glucosyltransferase phosphatase; UDPglucose-glycogen glucosyltransferase phosphatase; glycogen glucosyltransferase phosphatase; glycogen synthase D phosphatase; Mg2+ dependent glycogen synthase phosphatase; phosphatase type 2°C
Systematic name: [UDP-glucose:glycogen 4-α-D-glucosyltransferase-D] phosphohydrolase
Comments: The product is EC 2.4.1.11 glycogen(starch) synthase.
References: [6]

[EC 3.1.3.42 created 1976]

EC 3.1.3.43
Accepted name: [pyruvate dehydrogenase (acetyl-transferring)]-phosphatase
Reaction: [pyruvate dehydrogenase (acetyl-transferring)] phosphate + H2O = [pyruvate dehydrogenase (acetyl-transferring)] + phosphate
Other name(s): pyruvate dehydrogenase phosphatase; phosphopyruvate dehydrogenase phosphatase; [pyruvate dehydrogenase (lipoamide)]-phosphatase; [pyruvate dehydrogenase (lipoamide)]-phosphate phosphohydrolase
Systematic name: [pyruvate dehydrogenase (acetyl-transferring)]-phosphate phosphohydrolase
Comments: A mitochondrial enzyme associated with EC 1.2.4.1 pyruvate dehydrogenase (acetyl-transferring), in the pyruvate dehydrogenase complex.
References: [1476, 2083]
EC 3.1.3.44
Accepted name: [acetyl-CoA carboxylase]-phosphatase
Reaction: [acetyl-CoA carboxylase] phosphate + H2O = [acetyl-CoA carboxylase] + phosphate
Systematic name: [acetyl-CoA:carbon-dioxide ligase (ADP-forming)]-phosphate phosphohydrolase
Comments: Simultaneously dephosphorylates and activates EC 6.4.1.2 acetyl-CoA carboxylase. Acts similarly on EC 1.1.1.88 (hydroxymethylglutaryl-CoA reductase), EC 2.4.1.1 (phosphorylase), EC 2.4.1.11 [glycogen(starch) synthase], and dephosphorylates phosphoprotamine and 4-nitrophenyl phosphate. Not identical to EC 3.1.3.17 ([phosphorylase] phosphatase ) or EC 3.1.3.43 [pyruvate dehydrogenase (acetyl-transferring)]-phosphatase.
References: [1322]

EC 3.1.3.45
Accepted name: 3-deoxy-manno-octulosonate-8-phosphatase
Reaction: 3-deoxy-\(D\)-manno-octulosonate 8-phosphate + H2O = 3-deoxy-\(D\)-manno-octulosonate + phosphate
Systematic name: 3-deoxy-\(D\)-manno-octulosonate-8-phosphate 8-phosphohydrolase
References: [2071]

EC 3.1.3.46
Accepted name: fructose-2,6-bisphosphate 2-phosphatase
Reaction: \(\beta\)-d-fructose 2,6-bisphosphate + H2O = d-fructose 6-phosphate + phosphate
Other name(s): fructose-2,6-bisphosphatase; \(d\)-fructose-2,6-bisphosphate 2-phosphohydrolase
Systematic name: \(\beta\)-d-fructose-2,6-bisphosphate 2-phosphohydrolase
Comments: The enzyme copurifies with EC 2.7.1.105 6-phosphofructo-2-kinase. (cf. EC 3.1.3.54 fructose-2,6-bisphosphate 6-phosphatase).
References: [2229]

EC 3.1.3.47
Accepted name: [hydroxymethylglutaryl-CoA reductase (NADPH)]-phosphatase
Reaction: [hydroxymethylglutaryl-CoA reductase (NADPH)] phosphate + H2O = [hydroxymethylglutaryl-CoA reductase (NADPH)] + phosphate
Other name(s): reductase phosphatase
Systematic name: [hydroxymethylglutaryl-CoA reductase (NADPH)]-phosphate phosphohydrolase
Comments: Acts on the product of the reaction catalysed by EC 2.7.11.31 [hydroxymethylglutaryl-CoA reductase (NADPH)] kinase, simultaneously dephosphorylating and activating EC 1.1.1.34 hydroxymethylglutaryl-CoA reductase (NADPH).
References: [814, 815]

EC 3.1.3.48
Accepted name: protein-tyrosine-phosphatase
Reaction: protein tyrosine phosphate + H2O = protein tyrosine + phosphate
Other name(s): phosphotyrosine phosphatase; phosphoprotein phosphatase (phosphotyrosine); phosphotyrosine histone phosphatase; protein phosphotyrosine phosphatase; tyrosylprotein phosphatase; phosphotyrosine protein phosphatase; phosphorylsylprotein phosphatase; tyrosine O-phosphate phosphatase; PPT-phosphatase; PTPase; [phosphotyrosine]protein phosphatase; PTP-phosphatase

Systematic name: protein-tyrosine-phosphate phosphohydrolase

Comments: Dephosphorylates O-phosphotyrosine groups in phosphoproteins, such as the products of EC 2.7.10.2, non-specific protein-tyrosine kinase.

References: [715, 774]

[EC 3.1.3.48 created 1984]

EC 3.1.3.49

Accepted name: [pyruvate kinase]-phosphatase

Reaction: [pyruvate kinase] phosphate + H₂O = [pyruvate kinase] + phosphate

Other name(s): pyruvate kinase phosphatase

Systematic name: [ATP:pyruvate 2-O-phosphotransferase]-phosphate phosphohydrolase

Comments: Simultaneously dephosphorylates and activates EC 2.7.1.40 pyruvate kinase, that has been inactivated by protein kinase.

References: [1143]

[EC 3.1.3.49 created 1984]

EC 3.1.3.50

Accepted name: sorbitol-6-phosphatase

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

Other name(s): sorbitol-6-phosphate phosphatase

Systematic name: sorbitol-6-phosphate phosphohydrolase

Comments: Acts, very slowly, on hexose 6-phosphates.

References: [856]

[EC 3.1.3.50 created 1984]

EC 3.1.3.51

Accepted name: dolichyl-phosphatase

Reaction: dolichyl phosphate + H₂O = dolichol + phosphate

Other name(s): dolichol phosphate phosphatase; dolichol phosphatase; dolichol monophosphatase; dolichyl monophosphate phosphatase; dolichyl phosphate phosphatase; polyisoprenyl phosphate phosphatase; Dol-P phosphatase

Systematic name: dolichyl-phosphate phosphohydrolase

References: [18, 2115, 2765]

[EC 3.1.3.51 created 1984]

EC 3.1.3.52

Accepted name: [3-methyl-2-oxobutanoate dehydrogenase (2-methylpropanoyl-transferring)]-phosphatase

Reaction: [3-methyl-2-oxobutanoate dehydrogenase (2-methylpropanoyl-transferring)] phosphate + H₂O = [3-methyl-2-oxobutanoate dehydrogenase (2-methylpropanoyl-transferring)] + phosphate

Other name(s): branched-chain oxo-acid dehydrogenase phosphatase; branched-chain 2-keto acid dehydrogenase phosphatase; BCKDH; [3-methyl-2-oxobutanoate dehydrogenase (lipoamide)]-phosphatase; [3-methyl-2-oxobutanoate dehydrogenase (lipoamide)]-phosphate phosphohydrolase

Systematic name: [3-methyl-2-oxobutanoate dehydrogenase (2-methylpropanoyl-transferring)]-phosphate phosphohydrolase
Comments: A mitochondrial enzyme associated with the 3-methyl-2-oxobutanoate dehydrogenase complex. Simultaneously dephosphorylates and activates EC 1.2.4.4 3-methyl-2-oxobutanoate dehydrogenase (2-methylpropanoyl-transferring), that has been inactivated by phosphorylation.

References: [665, 2083]

[EC 3.1.3.52 created 1986]

EC 3.1.3.53
Accepted name: [myosin-light-chain] phosphatase
Other name(s): myosin light chain kinase phosphatase; myosin phosphatase; myosin phosphatase; protein phosphatase 2A; myosin-light-chain-phosphatase
Systematic name: [myosin-light-chain]-phosphate phosphohydrolase
Comments: The enzyme is composed of three subunits. The holoenzyme dephosphorylates myosin light chains and EC 2.7.11.18, myosin-light-chain kinase, but not myosin; the catalytic subunit acts on all three substrates.

References: [1943]

[EC 3.1.3.53 created 1986]

EC 3.1.3.54
Accepted name: fructose-2,6-bisphosphate 6-phosphatase
Reaction: β-D-fructose 2,6-bisphosphate + H₂O = β-D-fructofuranose 2-phosphate + phosphate
Other name(s): fructose-2,6-bisphosphate-6-phosphohydrolase; fructose-2,6-bisphosphate 6-phosphohydrolase; D-fructose-2,6-bisphosphate 6-phosphohydrolase
Systematic name: β-D-fructose-2,6-bisphosphate 6-phosphohydrolase
Comments: cf. EC 3.1.3.46 fructose-2,6-bisphosphate 2-phosphatase.

References: [2025, 2026]

[EC 3.1.3.54 created 1989]

EC 3.1.3.55
Accepted name: caldesmon-phosphatase
Reaction: caldesmon phosphate + H₂O = caldesmon + phosphate
Other name(s): SMP-I; smooth muscle caldesmon phosphatase
Systematic name: caldesmon-phosphate phosphohydrolase
Comments: Dephosphorylation activates the calmodulin- and actin-binding ability of the protein caldesmon.

References: [1801]

[EC 3.1.3.55 created 1989]

EC 3.1.3.56
Accepted name: inositol-polyphosphate 5-phosphatase
Reaction: (1) D-myo-inositol 1,4,5-trisphosphate + H₂O = myo-inositol 1,4-bisphosphate + phosphate
(2) 1D-myo-inositol 1,3,4,5-tetrakisphosphate + H₂O = 1D-myo-inositol 1,3,4-trisphosphate + phosphate
Other name(s): type I inositol-polyphosphate phosphatase; inositol trisphosphate phosphomonoesterase; InsP₃/Ins(1,3,4,5)P₄ 5-phosphatase; inosine triphosphatase; D-myo-inositol 1,4,5-trisphosphate 5-phosphatase; D-myo-inositol 1,4,5-trisphosphate 5-phosphatase; 1-myo-inositol 1,4,5-trisphosphate phosphomonoesterase; inositol phosphate 5-phosphomonoesterase; inositol-1,4,5-trisphosphate/1,3,4,5-tetrakisphosphate 5-phosphatase; Ins(1,4,5)P₃ 5-phosphatase; D-myo-inositol(1,4,5)/(1,3,4,5)-polyphosphate 5-phosphatase; inositol 1,4,5-trisphosphate phosphatase; inositol polyphosphate-5-phosphatase; myo-inositol-1,4,5-trisphosphate 5-phosphatase; inositol-1,4,5-trisphosphate 5-phosphatase

[EC 3.1.3.56 created 1989]
Systematic name: 1D-myoinositol-1,4,5-trisphosphate 5-phosphohydrolase
Comments: One mammalian isoform is known. This enzyme is distinguished from the family of enzymes classified under EC 3.1.3.36, phosphoinositide 5-phosphatase, by its inability to dephosphorylate inositol lipids.
References: [573, 639, 2825, 2689]

[EC 3.1.3.56 created 1989, modified 2002]

EC 3.1.3.57
Accepted name: inositol-1,4-bisphosphate 1-phosphatase
Reaction: 1D-myoinositol 1,4-bisphosphate + H2O = 1D-myoinositol 4-phosphate + phosphate
Other name(s): inositol-polyphosphate 1-phosphatase
Systematic name: 1D-myoinositol-1,4-bisphosphate 1-phosphohydrolase
Comments: The enzyme acts on inositol 1,4-bisphosphate and inositol 1,3,4-trisphosphate (forming inositol 3,4-bisphosphate) with similar \( V_{\text{max}} \) values for both substrates, but with a five-times higher affinity for the bisphosphate. Does not act on inositol 1-phosphate, inositol 1,4,5-trisphosphate or inositol 1,3,4,5-tetrakisphosphate.
References: [181, 432, 1092]

[EC 3.1.3.57 created 1989, modified 2002]

EC 3.1.3.58
Accepted name: sugar-terminal-phosphatase
Reaction: D-glucose 6-phosphate + H2O = D-glucose + phosphate
Other name(s): xylitol-5-phosphatase
Systematic name: sugar-\( \omega \)-phosphate phosphohydrolase
Comments: Acts on sugars and polyols phosphorylated on the terminal carbon, with a preference for sugars with a D-erythro-configuration, e.g. good substrates are glucose 6-phosphate, mannose 6-phosphate, 6-phosphogluconate, erythrose 4-phosphate and xylitol 5-phosphate.
References: [1495]

[EC 3.1.3.58 created 1989]

EC 3.1.3.59
Accepted name: alkylacetylglycerophosphatase
Other name(s): 1-alkyl-2-lyso-sn-glycero-3-P:acyetyl-CoA acetyltransferase; alkylacetylglycerophosphate phosphatase
Systematic name: 1-alkyl-2-acetyl-sn-glycerol-3-phosphate phosphohydrolase
Comments: Inolved in the biosynthesis of thrombocyte activating factor in animal tissues.
References: [1408]

[EC 3.1.3.59 created 1989]

EC 3.1.3.60
Accepted name: phosphoenolpyruvate phosphatase
Reaction: phosphoenolpyruvate + H2O = pyruvate + phosphate
Other name(s): PEP phosphatase
Systematic name: phosphoenolpyruvate phosphohydrolase
Comments: Also acts, but more slowly, on a wide range of other monophosphates.
References: [593, 1545, 1546]

[EC 3.1.3.60 created 1992]
EC 3.1.3.62
Accepted name: multiple inositol-polyphosphate phosphatase
Reaction: myo-inositol hexakisphosphate + H$_2$O = myo-inositol pentakisphosphate (mixed isomers) + phosphate
Other name(s): inositol (1,3,4,5)-tetrakisphosphate 3-phosphatase; inositol 1,3,4,5-tetrakisphosphate 3-phosphomonoesterase; inositol 1,3,4,5-tetrakisphosphate-5-phosphomonoesterase; inositol tetrakisphosphate phosphomonoesterase; inositol-1,3,4,5-tetrakisphosphate 3-phosphatase; MIPP
Systematic name: 1D-myoinositol-hexakisphosphate 5-phosphohydrolase
Comments: This enzyme exists in two isoforms. It also acts on Ins(1,3,4,5)$P_4$ to yield Ins(1,4,5)$P_3$.
References: [462, 450]

[EC 3.1.3.62 created 1992, modified 2002]

EC 3.1.3.63
Accepted name: 2-carboxy-d-arabinitol-1-phosphatase
Reaction: 2-carboxy-d-arabinitol 1-phosphate + H$_2$O = 2-carboxy-d-arabinitol + phosphate
Other name(s): 2-carboxyarabinitol 1-phosphatase; 2-carboxy-d-arabinitol 1-phosphate phosphohydrolase
Systematic name: 2-carboxy-d-arabinitol-1-phosphate 1-phosphohydrolase
References: [2196]

[EC 3.1.3.63 created 1992]

EC 3.1.3.64
Accepted name: phosphatidylinositol-3-phosphatase
Reaction: 1-phosphatidyl-1d-myoinositol 3-phosphate + H$_2$O = 1-phosphatidyl-1d-myoinositol + phosphate
Other name(s): inositol-1,3-bisphosphate 3-phosphatase; inositol 1,3-bisphosphate phosphatase; inositol-polyphosphate 3-phosphatase; D-myoinositol-1,3-bisphosphate 3-phosphohydrolase; phosphatidyl-3-phosphate 3-phosphohydrolase
Systematic name: 1-phosphatidyl-1d-myoinositol-3-phosphate 3-phosphohydrolase
Comments: This enzyme still works when the 2,3-bis(acyloxy)propyl group is removed, i.e., it hydrolyses Ins(1,3)$P_2$ to Ins-1-$P$.
References: [1478, 325]

[EC 3.1.3.64 created 1992, [EC 3.1.3.65 created 1992, incorporated 2002], modified 2002]]

[3.1.3.65 Deleted entry. inositol-1,3-bisphosphate 3-phosphatase. Now included with EC 3.1.3.64, phosphatidylinositol-3-phosphatase]

[EC 3.1.3.65 created 1992, deleted 2002]

EC 3.1.3.66
Accepted name: phosphatidylinositol-3,4-bisphosphate 4-phosphatase
Reaction: 1-phosphatidyl-myoinositol 3,4-bisphosphate + H$_2$O = 1-phosphatidyl-1d-myoinositol 3-phosphate + phosphate
Other name(s): inositol-3,4-bisphosphate 4-phosphatase; D-myoinositol-3,4-bisphosphate 4-phosphohydrolase; phosphoinositide 4-phosphatase; inositol polyphosphate 4-phosphatase; D-myoinositol-3,4-bisphosphate 4-phosphohydrolase; inositol polyphosphate 4-phosphatase type II
Systematic name: 1-phosphatidyl-1d-myoinositol-3,4-bisphosphate 4-phosphohydrolase
Comments: Mg$^{2+}$-independent. This enzyme still works when the 2,3-bis(acyloxy)propyl group is removed, i.e., it hydrolyses Ins(1,3,4)$P_3$ to Ins(1,3)$P_2$. It also converts Ins(3,4)$P_2$ into Ins-3-$P$.
References: [1051, 1831, 1830]
EC 3.1.3.66

Accepted name: phosphatidylinositol-3,4,5-trisphosphate 3-phosphatase
Reaction: phosphatidylinositol 3,4,5-trisphosphate + H₂O = phosphatidylinositol 4,5-bisphosphate + phosphate
Other name(s): PTEN, MMAC1; phosphatidylinositol-3,4,5-trisphosphate 3-phosphohydrolase
Systematic name: 1-phosphatidyl-1-D-myoinositol-3,4,5-trisphosphate 3-phosphohydrolase
Comments: Requires Mg²⁺. Does not dephosphorylate inositol 4,5-bisphosphate. This enzyme still works when the 2,3-bis(acyloxy)propyl group is removed, i.e., it hydrolyses Ins(1,3,4,5)P₄ to Ins(1,4,5)P₃
References: [1172, 2471]

EC 3.1.3.67

Accepted name: 2-deoxyglucose-6-phosphatase
Reaction: 2-deoxy-D-glucose 6-phosphate + H₂O = 2-deoxy-D-glucose + phosphate
Other name(s): 2-deoxyglucose-6-phosphate phosphatase
Systematic name: 2-deoxy-D-glucose-6-phosphate phosphohydrolase
Comments: Also active towards fructose 1-phosphate
References: [1153, 2056]

EC 3.1.3.68

Accepted name: glucosylglycerol 3-phosphatase
Reaction: 2-(β-D-glucoyl)-sn-glycerol-3-phosphate + H₂O = 2-(β-D-glucoyl)-sn-glycerol + phosphate
Other name(s): salt tolerance protein A, StpA
Systematic name: 2-(β-D-glucoyl)-sn-glycerol-3-phosphate phosphohydrolase
Comments: Acts with EC 2.4.1.213 (glucosylglycerol-phosphate synthase) to form glucosylglycerol, an osmolyte that endows cyanobacteria with resistance to salt.
References: [902, 903, 904]

EC 3.1.3.69

Accepted name: mannosyl-3-phosphoglycerate phosphatase
Reaction: 2(α-D-mannosyl)-3-phosphoglycerate + H₂O = 2(α-D-mannosyl)-D-glycerate + phosphate
Systematic name: α-D-mannosyl-3-phosphoglycerate phosphohydrolase
Comments: Requires Mg²⁺. The enzyme from Pyrococcus horikoshii is specific for α-D-mannosyl-3-phosphoglycerate and forms part of the pathway for the synthesis of mannosylglycerate.
References: [626]

EC 3.1.3.70

Accepted name: (2R)-2-phosphosulfolactate phosphatase
Reaction: (2R)-2-phospho-3-sulfolactate + H₂O = (2R)-3-sulfolactate + phosphate
Other name(s): (2R)-phosphosulfolactate phosphohydrolase; ComB phosphatase
Systematic name: (R)-2-phospho-3-sulfolactate phosphohydrolase

EC 3.1.3.71

Accepted name: 2-phosphosulfolactate phosphatase
Reaction: (2R)-2-phospho-3-sulfolactate + H₂O = (2R)-3-sulfolactate + phosphate
Other name(s): (2R)-phosphosulfolactate phosphohydrolase; ComB phosphatase
Systematic name: (R)-2-phospho-3-sulfolactate phosphohydrolase
Comments: Requires Mg\(^{2+}\). The enzyme from *Methanococcus jannaschii* acts on both stereoisomers of the substrate and also hydrolyses a number of phosphate monoesters of (S)-2-hydroxy carboxylic acids, including 2-phosphomalate, 2-phospholactate and 2-phosphoglycolate. This enzyme can also hydrolyse phosphate monoesters of (R)-2-hydroxy carboxylic acids such as (S)-2-phospho-3-sulfolate and (R)-2-phosphomalate, which, presumably, bind to the enzyme in opposite orientations.

References: [854]

EC 3.1.3.72

Accepted name: 5-phytase

Reaction: *myo*-inositol hexakisphosphate + H\(_2\)O = 1L-*myo*-inositol 1,2,3,4,6-pentakisphosphate + phosphate

Systematic name: *myo*-inositol-hexakisphosphate 5-phosphohydrolase

Comments: The enzyme attacks the product of the above reaction more slowly to yield Ins(1,2,3)P\(_3\).

References: [145]

EC 3.1.3.73

Accepted name: α-ribazole phosphatase

Reaction: α-ribazole 5′-phosphate + H\(_2\)O = α-ribazole + phosphate

Other name(s): CobC

Systematic name: α-ribazole-5′-phosphate phosphohydrolase

Comments: In *Salmonella typhimurium* LT2, under anaerobic conditions, CobU (EC 2.7.7.62 and EC 2.7.1.156), CobT (EC 2.4.2.21), CobC (EC 3.1.3.73) and CobS (EC 2.7.8.26) catalyse reactions in the nucleotide loop assembly pathway, which convert adenosylcobinamide (AdoCbi) into adenosylcobalamin (AdoCbl). CobT and CobC are involved in 5,6-dimethylbenzimidazole activation whereby 5,6-dimethylbenzimidazole is converted to its riboside, α-ribazole. The second branch of the nucleotide loop assembly pathway is the cobinamide (Cbi) activation branch where AdoCbi or adenosylcobinamide-phosphate is converted to the activated intermediate AdoCbi-GDP by the bifunctional enzyme CobU. CobS catalyses the final step in adenosylcobalamin biosynthesis, which is the condensation of AdoCbi-GDP with α-ribazole to yield adenosylcobalamin.

References: [1918, 2749]

EC 3.1.3.74

Accepted name: pyridoxal phosphatase

Reaction: pyridoxal 5′-phosphate + H\(_2\)O = pyridoxal + phosphate

Other name(s): vitamin B\(_6\) (pyridoxine) phosphatase; PLP phosphatase; vitamin B\(_6\)-phosphate phosphatase; PNP phosphatase

Systematic name: pyridoxal-5′-phosphate phosphohydrolase

Comments: Requires Mg\(^{2+}\). This enzyme is specific for phosphorylated vitamin B\(_6\) compounds: it acts not only on pyridoxal phosphate (PLP), but also on pyridoxine phosphate (PNP), pyridoxamine phosphate (PMP), 4-pyridoxic acid phosphate and 4-deoxypyridoxine phosphate. This reaction can also be carried out by EC 3.1.3.1 (alkaline phosphatase) and EC 3.1.3.2 (acid phosphatase), but these enzymes have very broad substrate specificities.

References: [711, 712, 1132]

EC 3.1.3.75

Accepted name: phosphoethanolamine/phosphocholine phosphatase
Reaction: (1) \( O\text{-phosphoethanolamine} + H_2O = \text{ethanolamine} + \text{phosphate} \)
(2) \( \text{phosphocholine} + H_2O = \text{choline} + \text{phosphate} \)

Other name(s): PHOSPHO1; 3X11A

Systematic name: phosphoethanolamine phosphohydrolase

Comments: Requires active site \( \text{Mg}^{2+} \) but also works, to a lesser extent, with \( \text{Co}^{2+} \) and \( \text{Mn}^{2+} \). The enzyme is highly specific for phosphoethanolamine and phosphocholine.

References: [1047, 2427, 2125]

[EC 3.1.3.75 created 2004]

EC 3.1.3.76

Accepted name: lipid-phosphate phosphatase

Reaction: \( (9\text{S},10\text{S})\text{-10-hydroxy-9-(phosphonoxy)octadecanoate} + H_2O = (9\text{S},10\text{S})\text{-9,10-dihydroxyoctadecanoate} + \text{phosphate} \)

Other name(s): hydroxy fatty acid phosphatase; dihydroxy fatty acid phosphatase; hydroxy lipid phosphatase; sEH (ambiguous); soluble epoxide hydrolase (ambiguous)

Systematic name: \( (9\text{S},10\text{S})\text{-10-hydroxy-9-(phosphonoxy)octadecanoate phosphohydrolase} \)

Comments: Requires \( \text{Mg}^{2+} \) for maximal activity. The enzyme from mammals is a bifunctional enzyme: the N-terminal domain exhibits lipid-phosphate-phosphatase activity and the C-terminal domain has the activity of EC 3.3.2.10, soluble epoxide hydrolase (sEH) [1799]. The best substrates for this enzyme are 10-hydroxy-9-(phosphonoxy)octadecanoates, with the \textit{threo} form being a better substrate than the \textit{erythro} form [1799]. The phosphatase activity is not found in plant sEH or in EC 3.3.2.9, microsomal epoxide hydrolase, from mammals [1799].

References: [1799, 455, 1711, 2592, 1798, 2408, 846]

[EC 3.1.3.76 created 2006]

EC 3.1.3.77

Accepted name: acireductone synthase

Reaction: \( 5\text{-(methylthio)-2,3-dioxopentyl phosphate} + H_2O = 1,2\text{-dihydroxy-5-(methylthio)pent-1-en-3-one} + \text{phosphate} \) (overall reaction)
(1a) \( 5\text{-}(methylthio)-2,3\text{-dioxopentyl phosphate} = 2\text{-hydroxy-5-(methylthio)-3-oxopent-1-enyl phosphate} \) (probably spontaneous)
(1b) \( 2\text{-hydroxy-5-(methylthio)-3-oxopent-1-enyl phosphate} + H_2O = 1,2\text{-dihydroxy-5-(methylthio)pent-1-en-3-one} + \text{phosphate} \)

Other name(s): E1; E-1 enolase-phosphatase

Systematic name: \( 5\text{-}(methylthio)-2,3\text{-dioxopentyl phosphate phosphohydrolase (isomerizing)} \)

Comments: This bifunctional enzyme first enolizes the substrate to form the intermediate 2-hydroxy-5-(methylthio)-3-oxopent-1-enyl phosphate, which is then dephosphorylated to form the acireductone 1,2-dihydroxy-5-(methylthio)pent-1-en-3-one [2826]. The acireductone represents a branch point in the methione-salvage pathway as it is used in the formation of formate, CO and 3-(methylthio)propanoate by EC 1.13.11.53 [acireductone dioxygenase (Ni\textsuperscript{2+}-requiring)] and of formate and 4-methylthio-2-oxobutanoate either by a spontaneous reaction under aerobic conditions or by EC 1.13.11.54 acireductone dioxygenase [iron(II)-requiring] [1745, 2826].

References: [1745, 2826, 2732]

[EC 3.1.3.77 created 2006]

EC 3.1.3.78

Accepted name: phosphatidylinositol-4,5-bisphosphate 4-phosphatase

Reaction: \( 1\text{-phosphatidyl-1\text{-d-myoinositol} 4,5\text{-bisphosphate} + H_2O = 1\text{-phosphatidyl-1\text{-d-myoinositol} 5-phosphate} + \text{phosphate} \)
Other name(s): phosphatidylinositol-4,5-bisphosphate 4-phosphatase I; phosphatidylinositol-4,5-bisphosphate 4-phosphatase II; type I PtdIns-4,5-P_2 4-Ptase; type II PtdIns-4,5-P_2 4-Ptase; LipD; PtdIns-4,5-P_2 4-phosphatase type I; PtdIns-4,5-P_2 4-phosphatase type II; type I phosphatidylinositol-4,5-bisphosphate 4-phosphatase; type 1 4-phosphatase

Systematic name: 1-phosphatidyl-1-D-myo-inositol-4,5-bisphosphate 4-phosphohydrolase

Comments: Two pathways exist in mammalian cells to degrade 1-phosphatidyl-1-D-myo-inositol 4,5-bisphosphate [PtdIns(4,5)P_2] [2644]. One is catalysed by this enzyme and the other by EC 3.1.3.36, phosphoinositide 5-phosphatase, where the product is PtdIns4P. The enzyme from human is specific for PtdIns(4,5)P_2 as substrate, as it cannot use PtdIns(3,4,5)P_3, PtdIns(3,4)P_2, PtdIns(3,5)P_2, PtdIns5P, PtdIns4P or PtdIns3P [2644]. In humans, the enzyme is localized to late endosomal/lysosomal membranes [2644]. It can control nuclear levels of PtdIns(5)P and thereby control p53-dependent apoptosis [2928].

References: [1805, 2644, 2928, 1585]

[EC 3.1.3.78 created 2008]

EC 3.1.3.79

Accepted name: mannosylfructose-phosphate phosphatase

Reaction: β-D-fructofuranosyl-α-D-mannopyranoside 6F-phosphate + H_2O = β-D-fructofuranosyl-α-D-mannopyranoside + phosphate

Other name(s): mannosylfructose-6-phosphate phosphatase; MFPP

Systematic name: β-D-fructofuranosyl-α-D-mannopyranoside-6F-phosphate phosphohydrolase

Comments: This enzyme, from the soil proteobacterium and plant pathogen Agrobacterium tumefaciens strain C58, requires Mg^{2+} for activity. Mannosylfructose is the major endogenous osmolyte produced by several α-proteobacteria in response to osmotic stress and is synthesized by the sequential action of EC 2.4.1.246 (mannosylfructose-phosphate synthase) followed by this enzyme. While mannosylfructose 6-phosphate is the physiological substrate, the enzyme can use sucrose 6-phosphate very efficiently. The F in mannosylfructose 6F-phosphate is used to indicate that the fructose residue of sucrose carries the substituent.

References: [2584]

[EC 3.1.3.79 created 2009]

EC 3.1.3.80

Accepted name: 2,3-bisphosphoglycerate 3-phosphatase

Reaction: 2,3-bisphospho-D-glycerate + H_2O = 2-phospho-D-glycerate + phosphate

Other name(s): MIPP1; 2,3-BPG 3-phosphatase

Systematic name: 2,3-bisphospho-D-glycerate 3-phosphohydrolase

Comments: This reaction is a shortcut in the Rapoport-Luebering shunt. It bypasses the reactions of EC 3.1.3.13/EC 5.4.2.1 (bisphosphoglycerate phosphatase/phosphoglycerate mutase) and directly forms 2-phospho-D-glycerate by removing the 3-phospho-group of 2,3-diphospho-D-glycerate [395]. The MIPP1 protein also catalyses the reaction of EC 3.1.3.62 (multiple inositol-polyphosphate phosphatase).

References: [395]

[EC 3.1.3.80 created 2010]

EC 3.1.3.81

Accepted name: diacylglycerol diphosphate phosphatase

Reaction: 1,2-diacyl-sn-glycerol 3-diphosphate + H_2O = 1,2-diacyl-sn-glycerol 3-phosphate + phosphate

Other name(s): DGPP phosphatase; DGPP phosphohydrolase; DPP1; DPPL1; DPPL2; PAP2; pyrophosphate phosphatase

Systematic name: 1,2-diacyl-sn-glycerol 3-phosphate phosphohydrolase
Comments: The bifunctional enzyme catalyses the dephosphorylation of diacylglycerol diphosphate to phosphatidate and the subsequent dephosphorylation of phosphatidate to diacylglycerol (cf. phosphatidate phosphatase (EC 3.1.3.4)). It regulates intracellular levels of diacylglycerol diphosphate and phosphatidate, phospholipid molecules believed to play a signaling role in stress response [916]. The phosphatase activity of the bifunctional enzyme is Mg\(^{2+}\)-independent and N-ethylmaleimide-insensitive and is distinct from the Mg\(^{2+}\)-dependent and N-ethylmaleimide-sensitive enzyme EC 3.1.3.4 (phosphatidate phosphatase) [339]. The diacylglycerol pyrophosphate phosphatase activity in *Saccharomyces cerevisiae* is induced by zinc depletion, by inositol supplementation, and when cells enter the stationary phase [1911].

References: [546, 545, 2831, 1911, 339, 916]

EC 3.1.3.82

**Accepted name:** D-glycero-\(\beta\)-D-manno-heptose 1,7-bisphosphate 7-phosphatase

**Reaction:**
\[
D\text{-glycero-}\beta\text{-d-manno-heptose 1,7-bisphosphate} + H_2O = D\text{-glycero-}\beta\text{-d-manno-heptose 1-phosphate} + phosphate
\]

**Other name(s):**
gmhB (gene name); yaeD (gene name)

**Systematic name:** D-glycero-\(\beta\)-D-manno-heptose 1,7-bisphosphate 7-phosphohydrolase

**Comments:** The enzyme is involved in biosynthesis of ADP-L-glycero-\(\beta\)-D-manno-heptose, which is utilized for assembly of the lipopolysaccharide inner core in Gram-negative bacteria. In vitro the catalytic efficiency with the \(\beta\)-anomer is 100-200-fold higher than with the \(\alpha\)-anomer [2734].

References: [1286, 2662, 2734]

EC 3.1.3.83

**Accepted name:** D-glycero-\(\alpha\)-D-manno-heptose 1,7-bisphosphate 7-phosphatase

**Reaction:**
\[
D\text{-glycero-}\alpha\text{-d-manno-heptose 1,7-bisphosphate} + H_2O = D\text{-glycero-}\alpha\text{-d-manno-heptose 1-phosphate} + phosphate
\]

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

**Systematic name:** D-glycero-\(\alpha\)-D-manno-heptose 1,7-bisphosphate 7-phosphohydrolase

**Comments:** The enzyme is involved in biosynthesis of GDP-L-glycero-\(\alpha\)-D-manno-heptose, which is required for assembly of S-layer glycoprotein in some Gram-positive bacteria. The in vitro catalytic efficiency of the enzyme from *Bacteroides thetaiotaomicron* is 6-fold higher with the \(\alpha\)-anomer than with the \(\beta\)-anomer [2734].

References: [2734]

EC 3.1.4 Phosphoric-diester hydrolases

EC 3.1.4.1

**Accepted name:** phosphodiesterase I

**Reaction:** Hydrolytically removes 5\(^{\prime}\)-nucleotides successively from the 3\(^{\prime}\)-hydroxy termini of 3\(^{\prime}\)-hydroxy-terminated oligonucleotides

**Other name(s):** 5\(^{\prime}\)-exonuclease; 5\(^{\prime}\)-phosphodiesterase; 5\(^{\prime}\)-nucleotide phosphodiesterase; oligonucleate 5\(^{\prime}\)-nucleotidohydrolase; 5\(^{\prime}\) nucleotide phosphodiesterase/alkaline phosphodiesterase I; 5\(^{\prime}\)-NPDase; 5\(^{\prime}\)-PDase; 5\(^{\prime}\)-PDE; 5\(^{\prime}\) NPDE; alkaline phosphodiesterase; nucleotide pyrophosphatase/phosphodiesterase I; orthophosphoric diester phosphohydrolase; PDE I; phosphodiesterase; exonuclease I; oligonucleate 5\(^{\prime}\)-nucleotidohydrolase

**Systematic name:** oligonucleotide 5\(^{\prime}\)-nucleotidohydrolase
**Comments:** Hydrolyses both ribonucleotides and deoxyribonucleotides. Has low activity towards polynucleotides. A 3'-phosphate terminus on the substrate inhibits hydrolysis.

**References:** [1245]

[EC 3.1.4.1 created 1961]

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**EC 3.1.4.2**

**Accepted name:** glycerophosphocholine phosphodiesterase  
**Reaction:** $sn$-glycero-3-phosphocholine + H$_2$O $\rightarrow$ choline + $sn$-glycerol 3-phosphate  
**Other name(s):** glycerophosphinococholine diesterase; glycerylphosphorylcholine diesterase; $sn$-glycero-3-phosphorylcholine diesterase; glycerolphosphorylcholine phosphodiesterase; glycerophosphohydrolase  
**Systematic name:** $sn$-glycero-3-phosphocholine glycerophosphohydrolase  
**Comments:** Also acts on $sn$-glycero-3-phosphoethanolamine.

**References:** [490, 958, 2763]

[EC 3.1.4.2 created 1961, modified 1976]

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**EC 3.1.4.3**

**Accepted name:** phospholipase C  
**Reaction:** a phosphatidylcholine + H$_2$O $\rightarrow$ 1,2-diacyl-$sn$-glycerol + choline phosphate  
**Other name(s):** lipophosphodiesterase I; lecithinase C; Clostridium welchii $\alpha$-toxin; Clostridium oedematiens $\beta$- and $\gamma$-toxins; lipophosphodiesterase C; phosphatidase C; heat-labile hemolysin; $\alpha$-toxin  
**Systematic name:** phosphatidylcholine cholinephosphohydrolase  
**Comments:** The bacterial enzyme, which is a zinc protein, also acts on sphingomyelin and phosphatidylinositol; that from seminal plasma does not act on phosphatidylinositol.

**References:** [585, 1479, 2296, 2491]

[EC 3.1.4.3 created 1961]

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**EC 3.1.4.4**

**Accepted name:** phospholipase D  
**Reaction:** a phosphatidylcholine + H$_2$O $\rightarrow$ choline + a phosphatidate  
**Other name(s):** lipophosphodiesterase II; lecithinase D; choline phosphatase  
**Systematic name:** phosphatidylcholine phosphatidohydrolase  
**Comments:** Also acts on other phosphatidyl esters.

**References:** [77, 614, 919, 2583]

[EC 3.1.4.4 created 1961]
3.1.4.10 Transferred entry. 1-phosphatidylinositol phosphodiesterase. Now EC 4.6.1.13, phosphatidylinositol diacylglycerol-lyase. As there is no hydrolysis of the inositol 1,2-cyclic phosphate formed, previous classification of the enzyme as a hydrolase was incorrect.

EC 3.1.4.11
Accepted name: phosphoinositide phospholipase C
Reaction: 1-phosphatidyl-1-D-myo-inositol 4,5-bisphosphate + H₂O = 1D-myo-inositol 1,4,5-trisphosphate + diacylglycerol
Other name(s): triphosphoinositide phosphodiesterase; phosphoinositidase C; 1-phosphatidylinositol-4,5-bisphosphate phosphodiesterase; monophosphatidylinositol phosphodiesterase; phosphatidylinositol phospholipase C; PI-PLC; 1-phosphatidyl-D-myo-inositol-4,5-bisphosphate inositoltrisphosphohydrolase
Systematic name: 1-phosphatidyl-1-D-myo-inositol-4,5-bisphosphate inositoltrisphosphohydrolase
Comments: These enzymes form some of the cyclic phosphate Ins(cyclic1,2)P(4,5)P₂ as well as Ins(1,4,5)P₃. They show activity towards phosphatidylinositol, i.e., the activity of EC 4.6.1.13, phosphatidylinositol diacylglycerol-lyase, in vitro at high [Ca²⁺]. Four β-isoforms regulated by G-proteins, two γ-forms regulated by tyrosine kinases, four δ-forms regulated at least in part by calcium and an ε-form, probably regulated by the oncogene ras, have been found.
References: [572, 2558, 2102]

EC 3.1.4.12
Accepted name: sphingomyelin phosphodiesterase
Reaction: sphingomyelin + H₂O = N-acylsphingosine + choline phosphate
Other name(s): neutral sphingomyelinase
Systematic name: sphingomyelin cholinephosphohydrolase
Comments: Has very little activity on phosphatidylcholine.
References: [132, 367, 975, 1196]

EC 3.1.4.13
Accepted name: serine-ethanolaminephosphate phosphodiesterase
Reaction: serine phosphoethanolamine + H₂O = serine + ethanolamine phosphate
Other name(s): serine ethanolamine phosphodiester phosphodiesterase; SEP diesterase
Systematic name: serine-phosphoethanolamine ethanolaminephosphohydrolase
Comments: Acts only on those phosphodiesters that have ethanolamine as a component part of the molecule.
References: [906]

EC 3.1.4.14
Accepted name: [acyl-carrier-protein] phosphodiesterase
Reaction: holo-[acyl-carrier protein] + H₂O = 4'-phosphopantetheine + apo-[acyl-carrier protein]
Other name(s): ACP hydrolyase; ACP phosphodiesterase; AcpH; [acyl-carrier-protein] 4'-pantetheine-phosphohydrolase; holo-[acyl-carrier-protein] 4'-pantetheine-phosphohydrolase
Systematic name: holo-[acyl-carrier protein] 4'-pantetheine-phosphohydrolase
The enzyme cleaves acyl-[acyl-carrier-protein] species with acyl chains of 6-16 carbon atoms although it appears to demonstrate a preference for the unacylated acyl-carrier protein (ACP) and short-chain ACPs over the medium- and long-chain species [2551]. Deletion of the gene encoding this enzyme abolishes ACP prosthetic-group turnover in vivo [2551]. Activation of apo-ACP to form the holoenzyme is carried out by EC 2.7.8.7, holo-[acyl-carrier-protein] synthase.

References:
[2375, 2657, 2551]
[EC 3.1.4.19 created 1972, deleted 1978]

[EC 3.1.4.20 created 1972, deleted 1978]

[3.1.4.21] Transferred entry. single-stranded-nucleate endonuclease. Now EC 3.1.30.1, Aspergillus nuclease S1
[EC 3.1.4.21 created 1972, deleted 1978]

[3.1.4.22] Transferred entry. ribonuclease I. Now EC 3.1.27.5, pancreatic ribonuclease
[EC 3.1.4.22 created 1972, deleted 1978]

[3.1.4.23] Transferred entry. ribonuclease II. Now EC 3.1.27.1, ribonuclease T2
[EC 3.1.4.23 created 1972, deleted 1978]

[3.1.4.24] Deleted entry. endoribonuclease III
[EC 3.1.4.24 created 1972, deleted 1978]

[3.1.4.25] Transferred entry. exodeoxyribonuclease I. Now EC 3.1.11.1, exodeoxyribonuclease I
[EC 3.1.4.25 created 1972, deleted 1978]

[3.1.4.26] Deleted entry. exodeoxyribonuclease II
[EC 3.1.4.26 created 1972, deleted 1978]

[3.1.4.27] Transferred entry. exodeoxyribonuclease III. Now EC 3.1.11.2, exodeoxyribonuclease III
[EC 3.1.4.27 created 1972, deleted 1978]

[3.1.4.28] Transferred entry. exodeoxyribonuclease IV. Now EC 3.1.11.3, exodeoxyribonuclease (lambda-induced)
[EC 3.1.4.28 created 1972, deleted 1978]

[3.1.4.29] Deleted entry. oligodeoxyribonuclease exonuclease
[EC 3.1.4.29 created 1972, deleted 1978]

[EC 3.1.4.30 created 1972, deleted 1978]

[3.1.4.31] Transferred entry. DNA 5′-dinucleotidohydrolase. Now EC 3.1.11.4, exodeoxyribonuclease (phage SP3-induced)
[EC 3.1.4.31 created 1972, deleted 1978]

[3.1.4.32] Deleted entry. endodeoxyribonuclease (ATP- and S-adenosylmethionine-dependent). See EC 3.1.21.3 type I site-specific deoxyribonuclease and EC 3.1.21.5 type III site-specific deoxyribonuclease
[EC 3.1.4.32 created 1972, deleted 1978]

[3.1.4.33] Deleted entry. endodeoxyribonuclease (ATP-hydrolysing). See EC 3.1.21.3 type I site-specific deoxyribonuclease and EC 3.1.21.5 type III site-specific deoxyribonuclease
[EC 3.1.4.33 created 1972, deleted 1978]

[3.1.4.34] Deleted entry. hybrid nuclease. See subclasses EC 3.1.15, EC 3.1.16, EC 3.1.30 and EC 3.1.31
[EC 3.1.4.34 created 1972, deleted 1978]
EC 3.1.4.35

**Accepted name:** 3′,5′-cyclic-GMP phosphodiesterase

**Reaction:** guanosine 3′,5′-cyclic phosphate + H₂O = guanosine 5′-phosphate

**Other name(s):** guanosine cyclic 3′,5′-phosphate phosphodiesterase; cyclic GMP phosphodiesterase; cyclic 3′,5′-GMP phosphodiesterase; cyclic guanosine 3′,5′-monophosphate phosphodiesterase; cyclic guanosine 3′,5′-phosphate phosphodiesterase; cGMP phosphodiesterase; cGMP-PDE; cyclic guanosine 3′,5′-phosphate phosphodiesterase

**Systematic name:** 3′,5′-cyclic-GMP 5′-nucleotidohydrolase

**References:** [1568]

[EC 3.1.4.35 created 1976]

[3.1.4.36 Deleted entry. 1,2-cyclic-inositol-phosphate phosphodiesterase. Now included with EC 3.1.4.43, glycerophosphoinositol inositolphosphodiesterase]

[EC 3.1.4.36 created 1976, deleted 2002]

EC 3.1.4.37

**Accepted name:** 2′,3′-cyclic-nucleotide 3′-phosphodiesterase

**Reaction:** nucleoside 2′,3′-cyclic phosphate + H₂O = nucleoside 2′-phosphate

**Other name(s):** cyclic-CMP phosphodiesterase; 2′,3′-cyclic AMP phosphodiesterase; cyclic 2′,3′-nucleotide 3′-phosphodiesterase; cyclic 2′,3′-nucleotide phosphodiesterase; 2′,3′-cyclic nucleoside monophosphate phosphodiesterase; 2′,3′-cyclic nucleotide 3′-phosphohydrolase; CNPase; 2′,3′-cyclic nucleotide phosphohydrolase; 2′,3′-cyclic nucleotide 3′-phosphodiesterase; 2′,3′-CNMP-3′-ase

**Systematic name:** nucleoside-2′,3′-cyclic-phosphate 2′-nucleotidohydrolase

**Comments:** The brain enzyme acts on 2′,3′-cyclic AMP more rapidly than on the UMP or CMP derivatives. An enzyme from liver acts on 2′,3′-cyclic CMP more rapidly than on the purine derivatives; it also hydrolysers the corresponding 3′,5′-cyclic phosphates, but more slowly. This latter enzyme has been called cyclic-CMP phosphodiesterase.

**References:** [583, 973, 974, 1358, 1820]

[EC 3.1.4.37 created 1976]

EC 3.1.4.38

**Accepted name:** glycerophosphocholine cholinephosphodiesterase

**Reaction:** sn-glycero-3-phosphocholine + H₂O = glycerol + choline phosphate

**Other name(s):** L-3-glycerolphosphinicocholine cholinephosphohydrolase

**Systematic name:** sn-glycero-3-phosphocholine cholinephosphohydrolase

**Comments:** No activity on sn-3-glycerophosphoethanolamine.

**References:** [7]

[EC 3.1.4.38 created 1976]

EC 3.1.4.39

**Accepted name:** alkylglycerophosphoethanolamine phosphodiesterase

**Reaction:** 1-alkyl-sn-glycero-3-phosphoethanolamine + H₂O = 1-alkyl-sn-glycerol 3-phosphate + ethanolamine

**Other name(s):** lysophospholipase D

**Systematic name:** 1-alkyl-sn-glycero-3-phosphoethanolamine ethanolaminehydrolase

**Comments:** Also acts on acyl and choline analogues.

**References:** [2833]

[EC 3.1.4.39 created 1976]

EC 3.1.4.40
Accepted name: CMP-N-acylneuramate phosphodiesterase
Reaction: CMP-N-acylneuramate + H₂O = CMP + N-acylneuramate
Other name(s): CMP-sialate hydrolase; CMP-sialic acid hydrolase; CMP-N-acylneuraminic acid hydrolase; cytidine monophosphosialic hydrolase; cytidine monophosphosialate hydrolase; cytidine monophosphate-N-acylneuraminic acid hydrolase; CMP-N-acylneuramate hydrolase
Systematic name: CMP-N-acylneuramate N-acylneuramino hydrolase
References: [1221]

[EC 3.1.4.40 created 1976]

EC 3.1.4.41
Accepted name: sphingomyelin phosphodiesterase D
Reaction: sphingomyelin + H₂O = ceramide phosphate + choline
Other name(s): sphingomyelinase D
Systematic name: sphingomyelin ceramide-phosphohydrolase
Comments: Does not act on phosphatidylcholine, but hydrolyses 2-lysophosphatidylcholine to choline and 2-lysophosphatidate.
References: [342, 2395]

[EC 3.1.4.41 created 1978]

EC 3.1.4.42
Accepted name: glycerol-1,2-cyclic-phosphate 2-phosphodiesterase
Reaction: glycerol 1,2-cyclic phosphate + H₂O = glycerol 1-phosphate
Other name(s): rac-glycerol 1,2-cyclic phosphate 2-phosphodiesterase
Systematic name: rac-glycerol-1,2-cyclic-phosphate 2-glycerophosphohydrolase
Comments: Acts on both stereoisomers of the substrate and also, more slowly, on 3′,5′-cyclic AMP and on 2′,3′-cyclic AMP.
References: [412]

[EC 3.1.4.42 created 1984]

EC 3.1.4.43
Accepted name: glycerophosphoinositol inositolphosphodiesterase
Reaction: 1-(sn-glycero-3-phospho)-1D-myoinositol + H₂O = myo-inositol + sn-glycerol 3-phosphate
Other name(s): 1,2-cyclic-inositol-phosphate phosphodiesterase; D-myoinositol 1,2-cyclic phosphate 2-phosphohydrolase; D-inositol 1,2-cyclic phosphate 2-phosphohydrolase; D-myoinositol 1,2-cyclic phosphate 2-phosphohydrolase; 1-D-myoinositol-1,2-cyclic-phosphate 2-inositolphosphohydrolase; inositol-1,2-cyclic-phosphate 2-inositolphosphohydrolase
Systematic name: 1-(sn-glycero-3-phospho)-1D-myoinositol inositolphosphohydrolase
Comments: This enzyme also hydrolyses Ins(cyclic1,2)P to Ins-1-P
References: [494, 492, 493, 2150]

[EC 3.1.4.43 created 1984, (EC 3.1.4.36 created 1976, incorporated 2002), modified 2002]

EC 3.1.4.44
Accepted name: glycerophosphoinositol glycerophosphodiesterase
Reaction: 1-(sn-glycero-3-phospho)-1D-myoinositol + H₂O = myo-inositol + sn-glycerol 3-phosphate
Other name(s): sn-glycero(3)phosphoinositol glycerophosphohydrolase; sn-glycero-3-phospho-1-inositol glycerophosphohydrolase
Systematic name: 1-(sn-glycero-3-phospho)-1D-myoinositol glycerophosphohydrolase
References: [495]
EC 3.1.4.45

Accepted name: N-acetylglucosamine-1-phosphodiester α-N-acetylg glucosaminidase

Reaction: glycoprotein N-acetyl-D-glucosaminyl-phospho-D-mannose + H₂O = N-acetyl-D-glucosamine + glycoprotein phospho-D-mannose

Other name(s): α-N-acetylg glucosaminyl phosphodiesterase; lysosomal α-N-acetylg glucosaminidase; phosphodiester glycosidase; α-N-acetyl-D-glucosamine-1-phosphodiester α-N-acetylglucosaminidase; 2-acetamido-2-deoxy-α-D-glucose 1-phosphodiester acetamidodeoxyglucohydrolase

Systematic name: glycoprotein-N-acetyl-D-glucosaminyl-phospho-D-mannose N-acetyl-D-glucosaminyl phosphohydrolase

Comments: Acts on a variety of compounds in which N-acetyl-D-glucosamine is α-linked to a phosphate group, including the biosynthetic intermediates of the high mannose oligosaccharide components of some lysosomal enzymes and the products of EC 2.7.8.17 UDP-N-acetylglucosamine—lysosomal-enzyme N-acetylglucosamine-phosphotransferase.

References: [520, 2667, 2669, 2710]

[EC 3.1.4.45 created 1984]

EC 3.1.4.46

Accepted name: glycerophosphodiester phosphodiesterase

Reaction: a glycerophosphodiester + H₂O = an alcohol + sn-glycerol 3-phosphate

Other name(s): gene hpd protein; glycerophosphoryl diester phosphodiesterase; IgD-binding protein D

Systematic name: glycerophosphodiester glycerophosphohydrolase

Comments: Broad specificity for glycerophosphodiesters; glycerophosphocholine, glycerophosphoethanolamine, glycerophosphoglycerol and bis(glycerophospho)-glycerol are hydrolysed.

References: [1381]

[EC 3.1.4.46 created 1986]

[3.1.4.47 Transferred entry. variant-surface-glycoprotein phospholipase C. Now EC 4.6.1.14, glycosylphosphatidylinositol diacylglycerol-lyase]

[EC 3.1.4.47 created 1989, deleted 2002]

EC 3.1.4.48

Accepted name: dolichylphosphate-glucose phosphodiesterase

Reaction: dolichyl β-D-glucosyl phosphate + H₂O = dolichyl phosphate + D-glucose

Other name(s): dolichol phosphoglucose phosphodiesterase; Dol-P-Glc phosphodiesterase

Systematic name: dolichyl-β-D-glucosyl-phosphate dolichylphosphohydrolase

References: [451]

[EC 3.1.4.48 created 1989]

EC 3.1.4.49

Accepted name: dolichylphosphate-mannose phosphodiesterase

Reaction: dolichyl β-D-mannosyl phosphate + H₂O = dolichyl phosphate + D-mannose

Other name(s): mannosylphosphodolichol phosphodiesterase

Systematic name: dolichyl-β-D-mannosyl-phosphate dolichylphosphohydrolase

References: [2575]

[EC 3.1.4.49 created 1990]
EC 3.1.4.50

Accepted name: glycosylphosphatidylinositol phospholipase D

Reaction: 6-(α-D-glucosaminyl)-1-phosphatidyl-1D-myoinositol + H₂O = 6-(α-D-glucosaminyl)-1D-myoinositol + 3-sn-phosphatidate

Other name(s): GPI-PLD; glycoprotein phospholipase D; phosphatidylinositol phospholipase D; phosphatidylinositol-specific phospholipase D

Systematic name: glycoprotein-phosphatidylinositol phosphatidohydrolase

Comments: This enzyme is also active when O-4 of the glucosamine is substituted by carrying the oligosaccharide that can link a protein to the structure. It therefore cleaves proteins from the lipid part of the glycosylphosphatidylinositol (GPI) anchors, but does so by hydrolysis, whereas glycosylphosphatidylinositol diacylglycerol-lyase (EC 4.6.1.14) does so by elimination. It acts on plasma membranes only after solubilization of the substrate with detergents or solvents, but it may act on intracellular membranes.

References: [1501, 1548, 1439, 507]

[EC 3.1.4.50 created 1990, modified 2002]

EC 3.1.4.51

Accepted name: glucose-1-phospho-D-mannosylglycoprotein phosphodiesterase

Reaction: 6-(D-glucose-1-phospho)-D-mannosylglycoprotein + H₂O = α-D-glucose 1-phosphate + D-mannosylglycoprotein

Other name(s): α-glucose-1-phosphate phosphodiesterase

Systematic name: 6-(D-glucose-1-phospho)-D-mannosylglycoprotein glucose-1-phosphohydrolase

Comments: The enzyme is specific for the product of EC 2.7.8.19 UDP-glucose—glycoprotein glucose phosphotransferase.

References: [2407]

[EC 3.1.4.51 created 1992]

EC 3.1.4.52

Accepted name: cyclic-guanylate-specific phosphodiesterase

Reaction: cyclic di-3′,5′-guanylate + H₂O = 5′-phosphoguanylyl(3′→5′)guanosine

Other name(s): cyclic bis(3′→5′)diguanylate phosphodiesterase; c-di-GMP-specific phosphodiesterase; c-di-GMP phosphodiesterase; phosphodiesterase; phosphodiesterase A1; PDEA1; VieA

Systematic name: cyclic bis(3′→5′)diguanylate 3′-nucleotidohydrolase

Comments: Requires Mg²⁺ or Mn²⁺ for activity and is inhibited by Ca²⁺ and Zn²⁺. Contains a heme unit. This enzyme linearizes cyclic di-3′,5′-guanylate, the product of EC 2.7.7.65, diguanylate cyclase and an allosteric activator of EC 2.4.1.12, cellulose synthase (UDP-forming), rendering it inactive [357]. It is the balance between these two enzymes that determines the cellular level of c-di-GMP [357].

References: [357, 400, 2247, 2508]

[EC 3.1.4.52 created 2008]

EC 3.1.4.53

Accepted name: 3′,5′-cyclic-AMP phosphodiesterase

Reaction: adenosine 3′,5′-cyclic phosphate + H₂O = adenosine 5′-phosphate

Other name(s): cAMP-specific phosphodiesterase; cAMP-specific PDE; PDE1; PDE2A; PDE2B; PDE4; PDE7; PDE8; PDEB1; PDEB2

Systematic name: 3′,5′-cyclic-AMP 5′-nucleotidohydrolase

Comments: Requires Mg²⁺ or Mn²⁺ for activity [102]. This enzyme is a class I phosphodiesterase that is specific for 3′,5′-cAMP and does not hydrolyse other nucleoside 3′,5′-cyclic phosphates such as cGMP (c.f. EC 3.1.4.17, 3′,5′-cyclic-nucleotide phosphodiesterase and EC 3.1.4.35, 3′,5′-cyclic-GMP phosphodiesterase). It is involved in modulation of the levels of cAMP, which is a mediator in the processes of cell transformation and proliferation [2063].

References: [37, 102, 2063, 1145, 1508]
EC 3.1.5 Triphosphoric-monoester hydrolases

**EC 3.1.5.1**

*Accepted name:* dGTPase  
*Reaction:* dGTP + H₂O = deoxyguanosine + triphosphate  
*Other name(s):* deoxy-GTPase; deoxyguanosine 5-triphosphate triphosphohydrolase; deoxyguanosine triphosphatase; deoxyguanosine triphosphate triphosphohydrolase  
*Systematic name:* dGTP triphosphohydrolase  
*Comments:* Also acts on GTP.  
*References:* [1312]

EC 3.1.6 Sulfuric-ester hydrolases

**EC 3.1.6.1**

*Accepted name:* arylsulfatase  
*Reaction:* a phenol sulfate + H₂O = a phenol + sulfate  
*Other name(s):* sulfatase; nitrocatechol sulfatase; phenolsulfatase; phenylsulfatase; p-nitrophenyl sulfatase; arylsulfate hydrolase; 4-methylumbelliferyl sulfatase; estrogen sulfatase; arylsulfatase C; arylsulfatase B; arylsulfatase A  
*Systematic name:* aryl-sulfate sulfohydrolase  
*Comments:* A group of enzymes with rather similar specificities.  
*References:* [556, 2157, 2158, 2760]

**EC 3.1.6.2**

*Accepted name:* steryl-sulfatase  
*Reaction:* 3β-hydroxyandrost-5-en-17-one 3-sulfate + H₂O = 3β-hydroxyandrost-5-en-17-one + sulfate  
*Other name(s):* arylsulfatase; steroid sulfatase; sterol sulfatase; dehydroepiandrosterone sulfate sulfatase; arylsulfatase C; steroid 3-sulfatase; steroid sulfate sulfohydrolase; dehydroepiandrosterone sulfate sulfatase; pregnenolone sulfatase; phenolic steroid sulfatase; 3-β-hydroxy steroid sulfate sulfatase  
*Systematic name:* steryl-sulfate sulfohydrolase  
*Comments:* Also acts on some related steryl sulfates.  
*References:* [2156, 2157, 2428]

**EC 3.1.6.3**

*Accepted name:* glycosulfatase  
*Reaction:* D-glucose 6-sulfate + H₂O = D-glucose + sulfate  
*Other name(s):* glucosulfatase  
*Systematic name:* sugar-sulfate sulfohydrolase  
*Comments:* Also acts on other sulfates of monosaccharides and disaccharides and on adenosine 5'-sulfate.  
*References:* [555, 608, 2157]
EC 3.1.6.4

**Accepted name:** N-acetylgalactosamine-6-sulfatase

**Reaction:** Hydrolysis of the 6-sulfate groups of the N-acetyl-D-galactosamine 6-sulfate units of chondroitin sulfate and of the D-galactose 6-sulfate units of keratan sulfate

**Other name(s):** chondroitin sulfatase; chondroitinase; galactose-6-sulfate sulfatase; acetylgalactosamine 6-sulfatase; N-acetylglactosamine-6-sulfate sulfatase; N-acetylgalactosamine 6-sulfatase

**Systematic name:** N-acetyl-D-galactosamine-6-sulfate 6-sulfohydrolase

**References:** [634, 828, 1459, 2390, 2904]

[EC 3.1.6.4 created 1961]

**Deleted entry. sinigrin sulfohydrolase; myrosulfatase**

[EC 3.1.6.5 created 1961, deleted 1964]

EC 3.1.6.6

**Accepted name:** choline-sulfatase

**Reaction:** choline sulfate + H₂O = choline + sulfate

**Systematic name:** choline-sulfate sulfohydrolase

**References:** [2498]

[EC 3.1.6.6 created 1965]

EC 3.1.6.7

**Accepted name:** cellulose-polysulfatase

**Reaction:** Hydrolysis of the 2- and 3-sulfate groups of the polysulfates of cellulose and charonin

**Systematic name:** cellulose-sulfate sulfohydrolase

**References:** [2487]

[EC 3.1.6.7 created 1965]

EC 3.1.6.8

**Accepted name:** cerebroside-sulfatase

**Reaction:** a cerebroside 3-sulfate + H₂O = a cerebroside + sulfate

**Other name(s):** arylsulfatase A; cerebroside sulfate sulfatase

**Systematic name:** cerebroside-3-sulfate 3-sulfohydrolase

**Comments:** Hydrolyses galactose-3-sulfate residues in a number of lipids. Also hydrolyses ascorbate 2-sulfate and many phenol sulfates.

**References:** [1628, 2158]

[EC 3.1.6.8 created 1972]

EC 3.1.6.9

**Accepted name:** chondro-4-sulfatase

**Reaction:** 4-deoxy-β-D-gluc-4-enuronosyl-(1→3)-N-acetyl-D-galactosamine 4-sulfate + H₂O = 4-deoxy-β-D-gluc-4-enuronosyl-(1→3)-N-acetyl-D-galactosamine + sulfate

**Other name(s):** chondroitin-4-sulfatase; 4-deoxy-β-D-gluc-4-enuronosyl-(1,3)-N-acetyl-D-galactosamine-4-sulfate 4-sulfohydrolase

**Systematic name:** 4-deoxy-β-D-gluc-4-enuronosyl-(1→3)-N-acetyl-D-galactosamine-4-sulfate 4-sulfohydrolase

**Comments:** Also acts on the saturated analogue but not on higher oligosaccharides, nor any 6-sulfates.

**References:** [972, 2158, 2844]

[EC 3.1.6.9 created 1972]
EC 3.1.6.10
Accepted name: chondro-6-sulfatase
Reaction: 4-deoxy-β-D-gluc-4-enuronosyl-(1→3)-N-acetyl-D-galactosamine 6-sulfate + H₂O = 4-deoxy-β-D-gluс-4-enuronosyl-(1→3)-N-acetyl-D-galactosamine + sulfate
Other name(s): 4-deoxy-β-D-gluc-4-enuronosyl-(1,3)-N-acetyl-D-galactosamine-6-sulfate 6-sulfohydrolase
Systematic name: 4-deoxy-β-D-gluc-4-enuronosyl-(1→3)-N-acetyl-D-galactosamine-6-sulfate 6-sulfohydrolase
Comments: Also acts on the saturated analogue and N-acetyl-D-galactosamine 4,6-disulfate, but not higher oligosaccharides, nor any 4-sulfate
References: [2844]

[EC 3.1.6.10 created 1972]

EC 3.1.6.11
Accepted name: disulfoglucosamine-6-sulfatase
Reaction: 2-N,6-O-disulfo-D-glucosamine + H₂O = 2-N-sulfo-D-glucosamine + sulfate
Other name(s): N-sulfoglucosamine-6-sulfatase; 6,N-sulfo-D-glucosamine 6-O-sulfohydrolase; N,6-O-disulfo-D-glucosamine 6-sulfohydrolase
Systematic name: 2-N,6-O-disulfo-D-glucosamine 6-sulfohydrolase
Comments: May be identical with EC 3.1.6.14 N-acetylgalactosamine-6-sulfatase.
References: [541]

[EC 3.1.6.11 created 1972, modified 1989]

EC 3.1.6.12
Accepted name: N-acetylgalactosamine-4-sulfatase
Reaction: Hydrolysis of the 4-sulfate groups of the N-acetyl-D-galactosamine 4-sulfate units of chondroitin sulfate and dermatan sulfate
Other name(s): chondroitinsulfatase; chondroitinase; arylsulfatase B; acetylgalactosamine 4-sulfatase; N-acetylgalactosamine 4-sulfate sulfohydrolase
Systematic name: N-acetyl-D-galactosamine-4-sulfate 4-sulfohydrolase
Comments: Acts also on N-acetylgalactosamine 4-sulfate.
References: [662, 852, 2607]

[EC 3.1.6.12 created 1984]

EC 3.1.6.13
Accepted name: iduronate-2-sulfatase
Reaction: Hydrolysis of the 2-sulfate groups of the L-iduronate 2-sulfate units of dermatan sulfate, heparan sulfate and heparin
Other name(s): chondroitinsulfatase; idurono-2-sulfatase; iduronate-2-sulfate sulfohydrolase; L-idurono-sulfatase; L-iduronosulfatase; L-iduronate 2-sulfate sulfohydrolase; sulfido-L-iduronate 2-sulfatase; sulfo-L-iduronate 2-sulfatase; L-iduronate 2-sulfate sulfohydrolase; iduronate-2-sulfate sulfohydrolase
Systematic name: L-iduronate-2-sulfate 2-sulfohydrolase
References: [64, 98, 548, 2903]

[EC 3.1.6.13 created 1984]

EC 3.1.6.14
Accepted name: N-acetylgalactosamine-6-sulfatase
Reaction: Hydrolysis of the 6-sulfate groups of the N-acetyl-D-glucosamine 6-sulfate units of heparan sulfate and keratan sulfate

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Other name(s): chondroitinsulfatase; O,N-disulfate O-sulfohydrolase; acetylglucosamine 6-sulfatase; N-acetylgalactosamine 6-sulfate sulfatase; acetylglucosamine 6-sulfatase; 2-acetamido-2-deoxy-D-glucose 6-sulfate sulfatase

Systematic name: N-acetyl-D-glucosamine-6-sulfate 6-sulfohydrolase

Comments: May be identical with EC 3.1.6.11 disulfoglucosamine-6-sulfatase.

References: [150, 1329, 2774]

[EC 3.1.6.14 created 1984]

EC 3.1.6.15

Accepted name: N-sulfoglucosamine-3-sulfatase
Reaction: Hydrolysis of the 3-sulfate groups of the N-sulfo-D-glucosamine 3-O-sulfate units of heparin

Other name(s): chondroitinsulfatase

Systematic name: N-sulfo-3-sulfoglucosamine 3-sulfohydrolase

Comments: The enzyme from Flavobacterium heparinum also hydrolyses N-acetyl-D-glucosamine 3-O-sulfate; the mammalian enzyme acts only on the disulfated residue.

References: [292, 1393]

[EC 3.1.6.15 created 1984, modified 1989]

EC 3.1.6.16

Accepted name: monomethyl-sulfatase
Reaction: monomethyl sulfate + H₂O = methanol + sulfate

Systematic name: monomethyl-sulfate sulfohydrolase

Comments: Highly specific; does not act on monoethyl sulfate, monoisopropyl sulfate or monododecyl sulfate.

References: [801]

[EC 3.1.6.16 created 1989]

EC 3.1.6.17

Accepted name: D-lactate-2-sulfatase
Reaction: (R)-2-O-sulfolactate + H₂O = (R)-lactate + sulfate

Other name(s): (S)-2-O-sulfolactate 2-sulfohydrolase (incorrect stereochemistry)

Systematic name: (R)-2-O-sulfolactate 2-sulfohydrolase

Comments: Highly specific.

References: [453]

[EC 3.1.6.17 created 1989]

EC 3.1.6.18

Accepted name: glucuronate-2-sulfatase
Reaction: Hydrolysis of the 2-sulfate groups of the 2-O-sulfo-D-glucuronate residues of chondroitin sulfate, heparin and heparitin sulfate

Other name(s): glucuronate-2-sulfatase

Systematic name: polysaccharide-2-O-sulfo-D-glucuronate 2-sulfohydrolase

Comments: Does not act on iduronate 2-sulfate residues (cf. EC 3.1.6.13 iduronate-2-sulfatase)

References: [2285]

[EC 3.1.6.18 created 1989]

EC 3.1.7 Diphosphoric-monoester hydrolases
EC 3.1.7.1

Accepted name: prenyl-diphosphatase
Reaction: prenyl diphosphate + H₂O = prenol + diphosphate
Other name(s): prenyl-pyrophosphatase; prenol pyrophosphatase; prenylphosphatase
Systematic name: prenyl-diphosphate diphosphohydrolase
Comments: Farnesyl diphosphate is the best substrate tested to date.
References: [2599]

[EC 3.1.7.1 created 1972]

EC 3.1.7.2

Accepted name: guanosine-3',5'-bis(diphosphate) 3'-diphosphatase
Reaction: guanosine 3',5'-bis(diphosphate) + H₂O = guanosine 5'-diphosphate + diphosphate
Other name(s): guanosine-3',5'-bis(diphosphate) 3'-pyrophosphatase; PpGpp-3'-pyrophosphohydrolase; PpGpp phosphohydrolase
Systematic name: guanosine-3',5'-bis(diphosphate) 3'-diphosphohydrolase
References: [971, 2109]

[EC 3.1.7.2 created 1980]

EC 3.1.7.3

Accepted name: monoterpenyl-diphosphatase
Reaction: a monoterpenyl diphosphate + H₂O = a monoterpenol + diphosphate
Other name(s): bornyl pyrophosphate hydrolase; monoterpenyl-pyrophosphatase
Systematic name: monoterpenyl-diphosphate diphosphohydrolase
Comments: A group of enzymes with varying specificity for the monoterpenol moiety. One has the highest activity on sterically hindered compounds such as (+)-bornyl diphosphate; another has highest activity on the diphosphates of primary allylic alcohols such as geraniol.
References: [458]

[EC 3.1.7.3 created 1984]

EC 3.1.7.4

Accepted name: sclareol cyclase
Reaction: geranylgeranyl diphosphate + 2 H₂O = sclareol + diphosphate
Other name(s): geranylgeranyl pyrophosphate:sclareol cyclase; geranylgeranyl pyrophosphate-sclareol cyclase; GGPP:sclareol cyclase
Systematic name: geranylgeranyl-diphosphate diphosphohydrolase (sclareol-forming)
Comments: Requires Mg²⁺ or Mn²⁺ for activity [889]. Sclareol, a labdane diterpene, is a plant secondary metabolite that exhibits potent antibacterial activity as well as fungal-growth-regulating and plant-growth-inhibiting properties. It also exhibits cytotoxic activity against human leukaemic cell lines by inducing apoptosis [547].
References: [120, 547, 889]

[EC 3.1.7.4 created 2008]

EC 3.1.7.5

Accepted name: geranylgeranyl diphosphate diphosphatase
Reaction: geranylgeranyl diphosphate + H₂O = geranylgeraniol + diphosphate
Other name(s): geranylgeranyl diphosphate phosphatase
Systematic name: geranyl-diphosphate diphosphohydrolase
Comments: Involved in the biosynthesis of plaunotol. There are two isoenzymes with different ion requirements. Neither require Mg²⁺ but in addition PII is inhibited by Zn²⁺, Mn²⁺ and Co²⁺. It is not known which isoenzyme is involved in plaunotol biosynthesis.

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EC 3.1.8 Phosphoric-triester hydrolases

EC 3.1.8.1
Accepted name: aryl dialkyl phosphatase
Reaction: an aryl dialkyl phosphate + H₂O = dialkyl phosphate + an aryl alcohol
Other name(s): organophosphate hydrolase; paraoxonase; A-esterase; aryltriphosphatase; organophosphate esterase; esterase B1; esterase E4; paraoxon esterase; pirimiphos-methyl oxon esterase; OPA anhydrase; organophosphorus hydrolase; phosphotriesterase; paraoxon hydrolase; OPH; organophosphorus acid anhydrase
Systematic name: aryltriphosphate dialkylphosphohydrolase
Comments: Acts on organophosphorus compounds (such as paraoxon) including esters of phosphonic and phosphinic acids. Inhibited by chelating agents; requires divalent cations for activity. Previously regarded as identical with EC 3.1.1.2 arylesterase.
References: [27, 244, 1523, 1534, 1]

EC 3.1.8.2
Accepted name: diisopropyl-fluorophosphatase
Reaction: diisopropyl fluorophosphate + H₂O = diisopropyl phosphate + fluoride
Other name(s): DFPase; tabunase; somanase; organophosphate acid anhydrase; organophosphate acid anhydrase; OPA anhydrase; diisopropylphosphofluoridase; dialkylfluorophosphatase; diisopropyl phosphorofluoridate hydrolase; isopropylphosphorofluoridase; diisopropylfluorophosphonate dehalogenase
Systematic name: diisopropyl-fluorophosphate fluorohydrolase
Comments: Acts on phosphorus anhydride bonds (such as phosphorus-halide and phosphorus-cyanide) in organophosphorus compounds (including ‘nerve gases’). Inhibited by chelating agents; requires divalent cations. Related to EC 3.1.8.1 aryl dialkyl phosphatase.
References: [84, 85, 86, 416, 1725, 1]

EC 3.1.11 Exodeoxyribonucleases producing 5′-phosphomonoesters

EC 3.1.11.1
Accepted name: exodeoxyribonuclease I
Reaction: Exonucleolytic cleavage in the 3′- to 5′-direction to yield nucleoside 5′-phosphates
Other name(s): Escherichia coli exonuclease I; E. coli exonuclease I; exonuclease I
Comments: Preference for single-stranded DNA. The Escherichia coli enzyme hydrolyses glucosylated DNA.
References: [215, 1226, 1415]

EC 3.1.11.2
Accepted name: exodeoxyribonuclease III
Reaction: Exonucleolytic cleavage in the 3′- to 5′-direction to yield nucleoside 5′-phosphates
Other name(s): Escherichia coli exonuclease III; E. coli exonuclease III; endoribonuclease III
Comments: Preference for double-stranded DNA. Has endonucleolytic activity near apurinic sites on DNA.
References: [1470, 2107, 2108]
EC 3.1.11.3
Accepted name: exodeoxyribonuclease (lambda-induced)
Reaction: Exonucleolytic cleavage in the 5′- to 3′-direction to yield nucleoside 5′-phosphates
Other name(s): lambda exonuclease; phage lambda-induced exonuclease; Escherichia coli exonuclease IV; E. coli exonuclease IV; exodeoxyribonuclease IV; exonuclease IV
Comments: Preference for double-stranded DNA. Does not attack single-strand breaks.
References: [1469, 1480]

EC 3.1.11.4
Accepted name: exodeoxyribonuclease (phage SP3-induced)
Reaction: Exonucleolytic cleavage in the 5′- to 3′-direction to yield nucleoside 5′-phosphates
Other name(s): phage SP3 DNase; DNA 5′-dinucleotidohydrolase; deoxyribonucleate 5′-dinucleotidase; deoxyribonucleic 5′-dinucleotidohydrolase; bacteriophage SP3 deoxyribonuclease; deoxyribonucleate 5′-dinucleotidase
Comments: Preference for single-stranded DNA.
References: [2596]

EC 3.1.11.5
Accepted name: exodeoxyribonuclease V
Reaction: Exonucleolytic cleavage in the presence of ATP in either 5′- to 3′- or 3′- to 5′-direction to yield 5′-phosphooligonucleotides
Other name(s): Escherichia coli exonuclease V; E. coli exonuclease V; gene recBC endoenzyme; RecBC deoxyribonuclease; gene recBC DNAse; exonuclease V; gene recBCD enzymes
Comments: Preference for double-stranded DNA. Possesses DNA-dependent ATPase activity. Acts endonucleolytically on single-stranded circular DNA.
References: [613, 845, 1889, 2827]

EC 3.1.11.6
Accepted name: exodeoxyribonuclease VII
Reaction: Exonucleolytic cleavage in either 5′- to 3′- or 3′- to 5′-direction to yield nucleoside 5′-phosphates
Other name(s): Escherichia coli exonuclease VII; E. coli exonuclease VII; endodeoxyribonuclease VII; exonuclease VII
Comments: Preference for single-stranded DNA.
References: [366, 365]

EC 3.1.13 Exoribonucleases producing 5′-phosphomonoesters

EC 3.1.13.1
Accepted name: exoribonuclease II
Reaction: Exonucleolytic cleavage in the 3′- to 5′-direction to yield nucleoside 5′-phosphates
Other name(s): ribonuclease II; ribonuclease Q; BN ribonuclease; Escherichia coli exo-RNase II; RNase II; exoribonuclease; 5′-exoribonuclease
Comments: Preference for single-stranded RNA. The enzyme processes 3′-terminal extra-nucleotides of monomeric tRNA precursors, following the action of EC 3.1.26.5 ribonuclease P.

References: [1834, 2249, 2305, 2401]

[EC 3.1.13.1 created 1972 as EC 3.1.4.20, transferred 1978 to EC 3.1.13.1]

EC 3.1.13.2

Accepted name: exoribonuclease H

Reaction: 3′-end directed exonucleolytic cleavage of viral RNA-DNA hybrid

Comments: This is a secondary reaction to the RNA 5′-end directed cleavage 13-19 nucleotides from the RNA end performed by EC 3.1.26.13 (retroviral ribonuclease H).

References: [2231]

[EC 3.1.13.2 created 1978, modified 2010]

EC 3.1.13.3

Accepted name: oligonucleotidase

Reaction: Exonucleolytic cleavage of oligonucleotides to yield nucleoside 5′-phosphates

Other name(s): oligoribonuclease

Comments: Also hydrolyses NAD+ to NMN and AMP.

References: [771]

[EC 3.1.13.3 created 1972 as EC 3.1.4.19, transferred 1978 to EC 3.1.13.3]

EC 3.1.13.4

Accepted name: poly(A)-specific ribonuclease

Reaction: Exonucleolytic cleavage of poly(A) to 5′-AMP

Other name(s): 3′-exoribonuclease; 2′,3′-exoribonuclease

Comments: Cleaves poly(A) in either the single- or double-stranded form.

References: [2258]

[EC 3.1.13.4 created 1984]

EC 3.1.13.5

Accepted name: ribonuclease D

Reaction: Exonucleolytic cleavage that removes extra residues from the 3′-terminus of tRNA to produce 5′-mononucleotides

Other name(s): RNase D

Comments: Requires divalent cations for activity (Mg2+, Mn2+ or Co2+). Alteration of the 3′-terminal base has no effect on the rate of hydrolysis whereas modification of the 3′-terminal sugar has a major effect. tRNA terminating with a 3′-phosphate is completely inactive [460]. This enzyme can convert a tRNA precursor into a mature tRNA [461].

References: [802, 461, 460, 2912]

[EC 3.1.13.5 created 2006]

EC 3.14 Exoribonucleases producing 3′-phosphomonoesters

EC 3.14.1

Accepted name: yeast ribonuclease

Reaction: Exonucleolytic cleavage to nucleoside 3′-phosphates
**Comments:** Similar enzyme: RNase U₄.

**References:** [1917]

[EC 3.1.14.1 created 1978]

**EC 3.1.15 Exonucleases that are active with either ribo- or deoxyribonucleic acids and produce 5’-phosphomonoesters**

**EC 3.1.15.1**

**Accepted name:** venom exonuclease

**Reaction:** Exonucleolytic cleavage in the 3’- to 5’-direction to yield nucleoside 5’-phosphates

**Other name(s):** venom phosphodiesterase

**Comments:** Preference for single-stranded substrate.

**References:** [1383]

[EC 3.1.15.1 created 1978]

**EC 3.1.16 Exonucleases that are active with either ribo- or deoxyribonucleic acids and produce 3’-phosphomonoesters**

**EC 3.1.16.1**

**Accepted name:** spleen exonuclease

**Reaction:** Exonucleolytic cleavage in the 5’- to 3’-direction to yield nucleoside 3’-phosphates

**Other name(s):** 3’-exonuclease; spleen phosphodiesterase; 3’-nucleotide phosphodiesterase; phosphodiesterase II

**Comments:** Preference for single-stranded substrate.

**References:** [178]

[EC 3.1.16.1 created 1972 as EC 3.1.4.18, transferred 1978 to EC 3.1.16.1]

**EC 3.1.21 Endodeoxyribonucleases producing 5’-phosphomonoesters**

**EC 3.1.21.1**

**Accepted name:** deoxyribonuclease I

**Reaction:** Endonucleolytic cleavage to 5’-phosphodinucleotide and 5’-phosphooligonucleotide end-products

**Other name(s):** pancreatic DNase; DNase; thymonuclease, dornase; dornava; dornavac; pancreatic deoxyribonuclease; pancreatic dornase; deoxyribonuclease (pancreatic); pancreatic DNase; DNAse; deoxyribonucleic phosphatase; DNase I; alkaline deoxyribonuclease; alkaline DNase; endodeoxyribonuclease I; DNA depolymerase; *Escherichia coli* endonuclease I; deoxyribonuclease A; DNA endonuclease; DNA nuclease

**Comments:** Preference for double-stranded DNA.

**References:** [497, 1347, 1384]


**EC 3.1.21.2**

**Accepted name:** deoxyribonuclease IV (phage-T₄-induced)

**Reaction:** Endonucleolytic cleavage to 5’-phosphoholigonucleotide end-products

**Other name(s):** endodeoxyribonuclease IV (phage T₄-induced); *E. coli* endonuclease IV; endodeoxyribonuclease; deoxyxendonuclease; deoxriboendonuclease; *Escherichia coli* endonuclease II; endonuclease II; DNA-adenine-transferase
Comments: Preference for single-stranded DNA.
References: [733, 734, 900, 2175]

[EC 3.1.21.2 created 1972 as EC 3.1.4.30, transferred 1978 to EC 3.1.21.2]

EC 3.1.21.3
Accepted name: type I site-specific deoxyribonuclease
Reaction: Endonucleolytic cleavage of DNA to give random double-stranded fragments with terminal 5’-phosphates; ATP is simultaneously hydrolysed
Other name(s): type I restriction enzyme; deoxyribonuclease (ATP- and S-adenosyl-L-methionine-dependent); restriction-modification system; deoxyribonuclease (adenosine triphosphate-hydrolyzing); adenosine triphosphate-dependent deoxyribonuclease; ATP-dependent DNase; type 1 site-specific deoxyribonuclease
Comments: This is a large group of enzymes which, together with those now listed as EC 3.1.21.4 (type II site-specific deoxyribonuclease) and EC 3.1.21.5 (type III site-specific deoxyribonuclease), were previously listed separately in sub-subclasses EC 3.1.23 and EC 3.1.24. They have an absolute requirement for ATP (or dATP) and S-adenosyl-L-methionine. They recognize specific short DNA sequences and cleave at sites remote from the recognition sequence. They are multifunctional proteins that also catalyse the reactions of EC 2.1.1.72 [site-specific DNA-methyltransferase (adenine-specific)] and EC 2.1.1.37
References: [2124]

[EC 3.1.21.3 created 1984 from EC 3.1.23 and EC 3.1.24]

EC 3.1.21.4
Accepted name: type II site-specific deoxyribonuclease
Reaction: Endonucleolytic cleavage of DNA to give specific double-stranded fragments with terminal 5’-phosphates
Other name(s): type II restriction enzyme
Comments: This is a large group of enzymes which, together with those now listed as EC 3.1.21.3 (type 1 site-specific deoxyribonuclease) and EC 3.1.21.5.
References: [2124]

[EC 3.1.21.4 created 1984 from EC 3.1.23 and EC 3.1.24]

EC 3.1.21.5
Accepted name: type III site-specific deoxyribonuclease
Reaction: Endonucleolytic cleavage of DNA to give specific double-stranded fragments with terminal 5’-phosphates
Other name(s): type III restriction enzyme; restriction-modification system
Comments: This is a large group of enzymes which, together with those now listed as EC 3.1.21.3 (type 1 site-specific deoxyribonuclease) and EC 3.1.21.4 (type II site-specific deoxyribonuclease), were previously listed separately in sub-subclasses EC 3.1.23 and EC 3.1.24. They have an absolute requirement for ATP but do not hydrolyse it; S-adenosy-L-methionine stimulates the reaction, but is not absolutely required. They recognize specific, short DNA sequences and cleave a short distance away from the recognition sequence. These enzymes exist as complexes with enzymes of similar specificity listed under EC 2.1.1.72 [site-specific DNA-methyltransferase (adenine-specific)] or EC 2.1.1.73
References: [2124]

[EC 3.1.21.5 created 1984 from EC 3.1.23 and EC 3.1.24]

EC 3.1.21.6
Accepted name: CC-preferring endodeoxyribonuclease
Reaction: endonucleolytic cleavage to give 5′-phosphooligonucleotide end-products, with a preference for cleavage within the sequence CC

Other name(s): *Streptomyces glaucescens* exocytoplasmic dodeoxyribonuclease

Comments: Prefers CC sites in double-stranded circular and linear DNA. Greater affinity for double-stranded than single-stranded DNA. Produces nicks, generating double-stranded fragments with 5′- and/or 3′-protruding single-stranded tails. Requires magnesium ions for activity. The endonuclease from *Chlorella*-like green algae infected with NYs-1 virus 4[2834] may be the same enzyme.

References: [2834, 58]

[EC 3.1.21.6 created 1999]

EC 3.1.21.7

Accepted name: deoxyribonuclease V

Reaction: Endonucleolytic cleavage at apurinic or apyrimidinic sites to products with a 5′-phosphate

Other name(s): endodeoxyribonuclease V; DNase V; *Escherichia coli* endodeoxyribonuclease V

Comments: Previously classified erroneously as EC 3.1.22.3.

References: [786]

[EC 3.1.21.7 created 1978 as EC 3.1.22.3, transferred 2001 to EC 3.1.21.7]

**EC 3.1.22 Endodeoxyribonucleases producing 3′-phosphomonoesters**

EC 3.1.22.1

Accepted name: deoxyribonuclease II

Reaction: Endonucleolytic cleavage to nucleoside 3′-phosphates and 3′-phosphooligonucleotide end-products

Other name(s): DNase II; pancreatic DNase II; deoxyribonucleate 3′-nucleotidohydrolase; DNase II; pancreatic DNase II; acid deoxyribonuclease; acid DNase

Comments: Preference for double-stranded DNA.

References: [179]

[EC 3.1.22.1 created 1961 as EC 3.1.4.6, transferred 1978 to EC 3.1.22.1, modified 1981]

EC 3.1.22.2

Accepted name: *Aspergillus* deoxyribonuclease K₁

Reaction: Endonucleolytic cleavage to nucleoside 3′-phosphates and 3′-phosphooligonucleotide end-products

Other name(s): *Aspergillus* DNase K₁

Comments: Preference for single-stranded DNA.

References: [1518, 2312]

[EC 3.1.22.2 created 1978, modified 1981]

[3.1.22.3 Transferred entry. deoxyribonuclease V. Now EC 3.1.21.7, deoxyribonuclease V]

[EC 3.1.22.3 created 1978, deleted 2001]

EC 3.1.22.4

Accepted name: crossover junction endodeoxyribonuclease

Reaction: Endonucleolytic cleavage at a junction such as a reciprocal single-stranded crossover between two homologous DNA duplexes (Holliday junction)

Other name(s): Hje endonuclease; Holliday junction endonuclease CCE₁; Holliday junction resolvase; Holliday junction-cleaving endonuclease; Holliday junction-resolving endoribonuclease; RusA Holliday junction resolvase; RusA endonuclease; RuvC endonuclease; SpCCE₁ Holliday junction resolvase; crossover junction endoribonuclease; cruciform-cutting endonuclease; endo X3; endonuclease RuvC; endonuclease VII; endonuclease X3; resolving enzyme CCE₁

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Comments: The enzyme from *Saccharomyces cerevisiae* has no endonuclease or exonuclease activity on single-stranded or double-stranded DNA molecules that do not contain Holliday junctions.

References: [2469, 2300, 2284, 704, 1655]

[EC 3.1.22.4 created 1989, modified 2003]

**EC 3.1.22.5**

**Accepted name:** deoxyribonuclease X

**Reaction:** Endonucleolytic cleavage of supercoiled plasma DNA to linear DNA duplexes

**Other name(s):** *Escherichia coli* endodeoxyribonuclease; *Escherichia coli* endodeoxyribonuclease X

**Comments:** Preference for supercoiled DNA; little activity on linear double-stranded DNA. Inhibited by single-stranded DNA, ATP and AMP.

**References:** [803]

[EC 3.1.22.5 created 1992]

**EC 3.1.23 Site-specific endodeoxyribonucleases: cleavage is sequence specific (deleted sub-subclass)**

[3.1.23.1] *Transferred entry. endodeoxyribonuclease AluI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease*]

[EC 3.1.23.1 created 1978, deleted 1984]

[3.1.23.2] *Transferred entry. endodeoxyribonuclease AsuI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease*]

[EC 3.1.23.2 created 1978, deleted 1984]

[3.1.23.3] *Transferred entry. endodeoxyribonuclease Aval. Now EC 3.1.21.4, type II site-specific deoxyribonuclease*]

[EC 3.1.23.3 created 1978, deleted 1984]

[3.1.23.4] *Transferred entry. endodeoxyribonuclease AvaII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease*]

[EC 3.1.23.4 created 1978, deleted 1984]

[3.1.23.5] *Transferred entry. endodeoxyribonuclease Ball. Now EC 3.1.21.4, type II site-specific deoxyribonuclease*]

[EC 3.1.23.5 created 1978, deleted 1984]

[3.1.23.6] *Transferred entry. endodeoxyribonuclease BamHI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease*]

[EC 3.1.23.6 created 1978, deleted 1984]

[3.1.23.7] *Transferred entry. endodeoxyribonuclease BbvI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease*]

[EC 3.1.23.7 created 1978, deleted 1984]

[3.1.23.8] *Transferred entry. endodeoxyribonuclease BclI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease*]

[EC 3.1.23.8 created 1978, deleted 1984]

[3.1.23.9] *Transferred entry. endodeoxyribonuclease BglI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease*]

[EC 3.1.23.9 created 1978, deleted 1984]

[3.1.23.10] *Transferred entry. endodeoxyribonuclease BglII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease*]

[EC 3.1.23.10 created 1978, deleted 1984]

[3.1.23.11] *Transferred entry. endodeoxyribonuclease BpuI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease*]

[EC 3.1.23.11 created 1978, deleted 1984]

[3.1.23.12] *Transferred entry. endodeoxyribonuclease DpnI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease*]
[EC 3.1.23.12 created 1978, modified 1982, deleted 1984]

[3.1.23.13 Transferred entry. endodeoxyribonuclease EcoRI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.13 created 1978, deleted 1984]

[3.1.23.14 Transferred entry. endodeoxyribonuclease EcoRII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.14 created 1978, deleted 1984]

[3.1.23.15 Transferred entry. endodeoxyribonuclease HaeI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.15 created 1978, deleted 1984]

[3.1.23.16 Transferred entry. endodeoxyribonuclease HaeII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.16 created 1978, deleted 1984]

[3.1.23.17 Transferred entry. endodeoxyribonuclease HaeIII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.17 created 1978, deleted 1984]

[3.1.23.18 Transferred entry. endodeoxyribonuclease Hgal. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.18 created 1978, deleted 1984]

[3.1.23.19 Transferred entry. endodeoxyribonuclease HHaI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.19 created 1978, deleted 1984]

[3.1.23.20 Transferred entry. endodeoxyribonuclease HindII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.20 created 1978, deleted 1984]

[3.1.23.21 Transferred entry. endodeoxyribonuclease HindIII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.21 created 1978, deleted 1984]

[3.1.23.22 Transferred entry. endodeoxyribonuclease Hinfl. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.22 created 1978, deleted 1984]

[3.1.23.23 Transferred entry. endodeoxyribonuclease Hpal. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.23 created 1978, deleted 1984]

[3.1.23.24 Transferred entry. endodeoxyribonuclease HpaII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.24 created 1978, deleted 1984]

[3.1.23.25 Transferred entry. endodeoxyribonuclease HphI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.25 created 1978, deleted 1984]

[3.1.23.26 Transferred entry. endodeoxyribonuclease Kpnl. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.26 created 1978, deleted 1984]

[3.1.23.27 Transferred entry. endodeoxyribonuclease MboI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.27 created 1978, deleted 1984]

[3.1.23.28 Transferred entry. endodeoxyribonuclease MboII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.28 created 1978, deleted 1984]

[3.1.23.29 Transferred entry. endodeoxyribonuclease MnlI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease]

[EC 3.1.23.29 created 1978, deleted 1984]

[EC 3.1.23.30 created 1978, modified 1982, deleted 1984]

[3.1.23.31] Transferred entry. endodeoxyribonuclease PstI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.31 created 1978, deleted 1984]

[3.1.23.32] Transferred entry. endodeoxyribonuclease PvuI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.32 created 1978, modified 1982, deleted 1984]

[3.1.23.33] Transferred entry. endodeoxyribonuclease PvuII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.33 created 1978, deleted 1984]

[3.1.23.34] Transferred entry. endodeoxyribonuclease SacI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.34 created 1978, deleted 1984]

[3.1.23.35] Transferred entry. endodeoxyribonuclease SacII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.35 created 1978, deleted 1984]

[3.1.23.36] Transferred entry. endodeoxyribonuclease SacIII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.36 created 1978, deleted 1984]

[3.1.23.37] Transferred entry. endodeoxyribonuclease SalI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.37 created 1978, deleted 1984]

[3.1.23.38] Transferred entry. endodeoxyribonuclease SgrI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.38 created 1978, deleted 1984]


[EC 3.1.23.39 created 1978, deleted 1984]

[3.1.23.40] Transferred entry. endodeoxyribonuclease TaqII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.40 created 1978, deleted 1984]

[3.1.23.41] Transferred entry. endodeoxyribonuclease XbaI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.41 created 1978, deleted 1984]


[EC 3.1.23.42 created 1978, deleted 1984]

[3.1.23.43] Transferred entry. endodeoxyribonuclease XhoII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.43 created 1978, modified 1982, deleted 1984]

[3.1.23.44] Transferred entry. endodeoxyribonuclease Xmal. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.44 created 1978, deleted 1984]

[3.1.23.45] Transferred entry. endodeoxyribonuclease XniI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.45 created 1978, modified 1982, deleted 1984]

[3.1.23.46] Transferred entry. endodeoxyribonuclease AimI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

[EC 3.1.23.46 created 1982, deleted 1984]

[3.1.23.47] Transferred entry. endodeoxyribonuclease AccI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

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Transferred entry. endodeoxyribonuclease AceII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease AtuAl. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease AtuBVI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease AcaI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease AcyI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease AosI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease AsuII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease AvaIII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease AvrII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease Bce4579. Now EC 3.1.21.4, type II site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease Bce4579I (see http://rebase.neb.com/rebase/rebase.html)

Transferred entry. endodeoxyribonuclease Bce1229. Now EC 3.1.21.4, type II site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease Bce1229I (see http://rebase.neb.com/rebase/rebase.html)

Transferred entry. endodeoxyribonuclease Bme899. Now EC 3.1.21.4, type II site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease Bme899I (see http://rebase.neb.com/rebase/rebase.html)

Transferred entry. endodeoxyribonuclease Bme205. Now EC 3.1.21.4, type II site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease Bme205I (see http://rebase.neb.com/rebase/rebase.html)

Transferred entry. endodeoxyribonuclease BmeI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease Bsp1286. Now EC 3.1.21.4, type II site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease Bsp1286I (see http://rebase.neb.com/rebase/rebase.html)

Transferred entry. endodeoxyribonuclease BstAI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.
Transferred entry. endodeoxyribonuclease BstEII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease BstEIII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease BstPI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease BsuM. Now EC 3.1.21.4, type II site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease BsuMI (see http://rebase.neb.com/rebase/rebase.html).

Transferred entry. endodeoxyribonuclease Bsa6633. Now EC 3.1.21.4, type II site-specific deoxyribonuclease. The name was misprinted in supplement 3 of the 1978 edition. Assumed to be the same as endodeoxyribonuclease Bsa6633I (see http://rebase.neb.com/rebase/rebase.html).

Transferred entry. endodeoxyribonuclease Bsu1145. Now EC 3.1.21.4, type II site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease Bsu1145I (see http://rebase.neb.com/rebase/rebase.html).

Transferred entry. endodeoxyribonuclease Bsu1192. Now EC 3.1.21.4, type II site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease Bsu1192I or Bsu1192II (see http://rebase.neb.com/rebase/rebase.html).

Transferred entry. endodeoxyribonuclease Bsu1193. Now EC 3.1.21.4, type II site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease Bsu1193I (see http://rebase.neb.com/rebase/rebase.html).


Transferred entry. endodeoxyribonuclease Bsu1259. Assumed to be the same as endodeoxyribonuclease Bsu1259I (see http://rebase.neb.com/rebase/rebase.html).

Transferred entry. endodeoxyribonuclease Clal. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease CauII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease CviI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease Ddel. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.

Transferred entry. endodeoxyribonuclease EclII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease.
Transferred entry. endodeoxyribonuclease EcaI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease EcoRI'. Now EC 3.1.21.4, type II site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease EcoRI (see http://rebase.neb.com/rebase/rebase.html)

Transferred entry. endodeoxyribonuclease Fnu48I. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease Fnu4H. Now EC 3.1.21.4, type II site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease Fnu4HI (see http://rebase.neb.com/rebase/rebase.html)

Transferred entry. endodeoxyribonuclease HapI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease Hin1056II. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease HinfIII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease HgiAI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease HgiCI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease HgiDI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease HgiEII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease MstI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease MstII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease MglI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease MglII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease MnoIII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease MnnIII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease
Transferred entry. endodeoxyribonuclease MviI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease MviII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease OxaII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease PaeR7. Now EC 3.1.21.4, type II site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease PaeR7I (see http://rebase.neb.com/rebase/rebase.html)

Transferred entry. endodeoxyribonuclease Rspl. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease Rsal. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease SmaI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease SspI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease SnaI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease SfaNI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease SalII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease SauI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease SphiI. Now EC 3.1.21.4, type II site-specific deoxyribonuclease

Transferred entry. endodeoxyribonuclease XmaIII. Now EC 3.1.21.4, type II site-specific deoxyribonuclease
EC 3.1.24 Site specific endodeoxyribonucleases: cleavage is not sequence specific (deleted sub-subclass)

[3.1.24.1 Transferred entry. endodeoxyribonuclease EcoB. Now EC 3.1.21.3, type I site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease EcoBI (see http://rebase.neb.com/rebase/rebase.html)]

[EC 3.1.24.1 created 1978, modified 1982, deleted 1984]

[3.1.24.2 Transferred entry. endodeoxyribonuclease EcoK. Now EC 3.1.21.3, type I site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease EcoKI (see http://rebase.neb.com/rebase/rebase.html)]

[EC 3.1.24.2 created 1978, modified 1982, deleted 1984]

[3.1.24.3 Transferred entry. endodeoxyribonuclease EcoPI. Now EC 3.1.21.5, type III site-specific deoxyribonuclease. The name is misprinted in supplement 3 of the 1978 edition]

[EC 3.1.24.3 created 1978, modified 1982, deleted 1984]

[3.1.24.4 Transferred entry. endodeoxyribonuclease EcoP15. Now EC 3.1.21.5, type III site-specific deoxyribonuclease. Assumed to be the same as endodeoxyribonuclease EcoP15I (see http://rebase.neb.com/rebase/rebase.html)]

[EC 3.1.24.4 created 1978, modified 1982, deleted 1984]

EC 3.1.25 Site-specific endodeoxyribonucleases that are specific for altered bases

EC 3.1.25.1

Accepted name: deoxyribonuclease (pyrimidine dimer)

Reaction: Endonucleolytic cleavage near pyrimidine dimers to products with 5′-phosphate

Other name(s): endodeoxyribonuclease (pyrimidine dimer); endodeoxyribonuclease (pyrimidine dimer); bacterio-

Comments: Acts on a damaged strand, 5′ from the damaged site.

References: [257, 2104]

[EC 3.1.25.1 created 1978]

[3.1.25.2 Transferred entry. endodeoxyribonuclease (apurinic or apyrimidinic). Now EC 4.2.99.18, DNA-(apurinic or apyrimidinic site) lyase]

[EC 3.1.25.2 created 1978, deleted 1992]

EC 3.1.26 Endoribonucleases producing 5′-phosphomonoesters

EC 3.1.26.1

Accepted name: Physarum polycephalum ribonuclease

Reaction: Endonucleolytic cleavage to 5′-phosphomonoester

References: [1010]

[EC 3.1.26.1 created 1978]

EC 3.1.26.2

Accepted name: ribonuclease α

Reaction: Endonucleolytic cleavage to 5′-phosphomonoester

Other name(s): 2′-O-methyl RNase

Comments: Specific for O-methylated RNA.

References: [1833]

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EC 3.1.26.3

Accepted name: ribonuclease III

Reaction: Endonucleolytic cleavage to a 5'-phosphomonoester

Other name(s): RNase III; ribonuclease 3

Comments: This is an endoribonuclease that cleaves double-stranded RNA molecules [882]. The cleavage can be either a single-stranded nick or double-stranded break in the RNA, depending in part upon the degree of base-pairing in the region of the cleavage site [446]. Specificity is conferred by negative determinants, i.e., the presence of certain Watson-Crick base-pairs at specific positions that strongly inhibit cleavage [2913]. RNase III is involved in both rRNA processing and mRNA processing and decay.

References: [459, 2078, 2127, 882, 446, 2913]

EC 3.1.26.4

Accepted name: ribonuclease H

Reaction: Endonucleolytic cleavage to 5'-phosphomonoester

Other name(s): endoribonuclease H (calf thymus); RNase H; RNA-DNA hybrid ribonucleotidohydrolase; hybrid ribonuclease; hybridase; hybridase (ribonuclease H); ribonuclease H; hybrid nuclease; calf thymus ribonuclease H

Comments: Acts on RNA-DNA hybrids.

References: [898, 2415]

EC 3.1.26.5

Accepted name: ribonuclease P

Reaction: Endonucleolytic cleavage of RNA, removing 5'-extranucleotides from tRNA precursor

Comments: An RNA-containing enzyme, essential for tRNA processing; generates 5'-termini or mature tRNA molecules.

References: [193, 194, 2126]

EC 3.1.26.6

Accepted name: ribonuclease IV

Reaction: Endonucleolytic cleavage of poly(A) to fragments terminated by 3'-hydroxy and 5'-phosphate groups

Other name(s): endoribonuclease IV; poly(A)-specific ribonuclease

Comments: Forms oligonucleotides with an average chain length of 10.

References: [1729, 1730]

EC 3.1.26.7

Accepted name: ribonuclease P4

Reaction: Endonucleolytic cleavage of RNA, removing 3'-extranucleotides from tRNA precursor

References: [2277]
EC 3.1.26.8
Accepted name: ribonuclease M5
Reaction: Endonucleolytic cleavage of RNA, removing 21 and 42 nucleotides, respectively, from the 5′- and 3′-termini of a 5S-rRNA precursor
Other name(s): RNase M5; 5S ribosomal maturation nuclease; 5S ribosomal RNA maturation endonuclease
Comments: Converts the 5S-rRNA precursor from Bacillus subtilis into 5S-rRNA, with 5′-phosphate and 3′-hydroxy groups.
References: [2377]

EC 3.1.26.9
Accepted name: ribonuclease [poly-(U)-specific]
Reaction: Endonucleolytic cleavage of poly(U) to fragments terminated by 3′-hydroxy and 5′-phosphate groups
Other name(s): ribonuclease (uracil-specific); uracil-specific endoribonuclease; uracil-specific RNase
Comments: Forms oligonucleotides with chain lengths of 6 to 12.
References: [100]

EC 3.1.26.10
Accepted name: ribonuclease IX
Reaction: Endonucleolytic cleavage of poly(U) or poly(C) to fragments terminated by 3′-hydroxy and 5′-phosphate groups
Other name(s): poly(U)- and poly(C)-specific endoribonuclease
Comments: Acts on poly(U) and poly(C), with a higher affinity for poly(C), but does not act on poly(A) or poly(G).
References: [2318]

EC 3.1.26.11
Accepted name: tRNase Z
Reaction: Endonucleolytic cleavage of RNA, removing extra 3′ nucleotides from tRNA precursor, generating 3′-termini of tRNAs. A 3′-hydroxy group is left at the tRNA terminus and a 5′-phosphoryl group is left at the trailer molecule
Other name(s): 3′ tRNase; tRNA 3 endonuclease; RNase Z; 3′ tRNase
Comments: No cofactor requirements. An homologous enzyme to that found in Arabidopsis thaliana has been found in Methanococcus janaschii.
References: [2242, 1604, 2241, 1349, 1713, 1667, 2495]

EC 3.1.26.12
Accepted name: ribonuclease E
Reaction: Endonucleolytic cleavage of single-stranded RNA in A- and U-rich regions
Other name(s): endoribonuclease E; RNase E; Rne protein
RNase E is a bacterial ribonuclease that plays a role in the processing of ribosomal RNA (9S to 5S rRNA), the chemical degradation of bulk cellular RNA, the decay of specific regulatory, messenger and structural RNAs and the control of plasmid DNA replication [676]. The enzyme binds to monophosphorylated 5′ ends of substrates but exhibits sequential cleavages in the 3′ to 5′ direction [676]. 2′-O-Methyl nucleotide substitutions at RNase E binding sites do not prevent binding but do prevent cleavage of non-modified target sequences 5′ to that locus [676]. In *Escherichia coli*, the enzyme is found in the RNA degradosome. The C-terminal half of the protein contains binding sites for the three other major degradosomal components, the DEAD-box RNA helicase Rh1B, enolase (EC 4.1.1.11) and polynucleotide phosphorylase (EC 2.7.7.8).

References: [676, 612, 439, 2681, 2416, 326]

EC 3.1.26.13

**Accepted name:** retroviral ribonuclease H  
**Reaction:** Endohydrolysis of RNA in RNA/DNA hybrids. Three different cleavage modes: 1. sequence-specific internal cleavage of RNA [1-4]. Human immunodeficiency virus type 1 and Moloney murine leukemia virus enzymes prefer to cleave the RNA strand one nucleotide away from the RNA-DNA junction [5]. 2. RNA 5′-end directed cleavage 13-19 nucleotides from the RNA end [6,7]. 3. DNA 3′-end directed cleavage 15-20 nucleotides away from the primer terminus [8-10].

**Other name(s):** RT/RNase H; retroviral reverse transcriptase RNaseH; HIV RNase H  
**Comments:** Retroviral reverse transcriptase is a multifunctional enzyme responsible for viral replication. To perform this task the enzyme combines two distinct activities. The polymerase domain (EC 2.7.7.49, RNA-directed DNA polymerase) occupies the N-terminal two-thirds of the reverse transcriptase whereas the ribonuclease H domain comprises the C-terminal remaining one-third [355, 2262]. The RNase H domain of Moloney murine leukemia virus and Human immunodeficiency virus display two metal binding sites [831, 488, 1937].

References: [2263, 2206, 2065, 264, 2264, 527, 1210, 1305, 1355, 355, 2262, 831, 1937]

EC 3.1.27 Endoribonucleases producing 3′-phosphomonoesters

EC 3.1.27.1

**Accepted name:** ribonuclease T₂  
**Reaction:** Two-stage endonucleolytic cleavage to nucleoside 3′-phosphates and 3′-phosphoholigouucleotides with 2′,3′-cyclic phosphate intermediates

**Other name(s):** ribonuclease II; base-non-specific ribonuclease; nonbase-specific RNase; RNase (non-base specific); non-base specific ribonuclease; nonspecific RNase; RNase Ms; RNase M; RNase II; *Escherichia coli* ribonuclease II; ribonuclease nucleotido-2′-transferase (cyclizing); acid ribonuclease; RNAase CL; *Escherichia coli* ribonuclease I’ ribonuclease PP2; ribonuclease N₂; ribonuclease M; acid RNase; ribonuclease (non-base specific); ribonuclease (non-base specific); RNase T₂; ribonuclease PP3; ribonucleate 3′-oligouucleotide hydrolase; RNase II; ribonuclease U₄

References: [780, 987, 2081, 2635]

[EC 3.1.27.1 created 1972 as EC 3.1.4.23, transferred 1978 to EC 3.1.27.1, modified 1981]

EC 3.1.27.2

**Accepted name:** *Bacillus subtilis* ribonuclease  
**Reaction:** Endonucleolytic cleavage to 2′,3′-cyclic nucleotides

**Other name(s):** *Proteus mirabilis* RNase; ribonuclease nucleotido-2′-transferase (cyclizing)

References: [1815, 2851, 2852]
EC 3.1.27.3
Accepted name: ribonuclease T₁
Reaction: Two-stage endonucleolytic cleavage to nucleoside 3′-phosphates and 3′-phosphooligonucleotides ending in Gp with 2′,3′-cyclic phosphate intermediates
Other name(s): guanyloribonuclease; Aspergillus oryzae ribonuclease; RNase N₁; RNase N₂; ribonuclease N₃; ribonuclease U₁; ribonuclease F₁; ribonuclease Ch; ribonuclease P₁; ribonuclease SA; RNase F₁; ribonuclease C₂; ribonuclease U₂; RNase U₂; RNase U₃; ribonuclease (purine)
Comments: Formerly EC 2.7.7.26 and EC 3.1.4.8.
References: [1205, 2482]

EC 3.1.27.4
Accepted name: ribonuclease U₂
Reaction: Two-stage endonucleolytic cleavage to nucleoside 3′-phosphates and 3′-phosphooligonucleotides ending in Ap or Gp with 2′,3′-cyclic phosphate intermediates
Other name(s): purine specific endoribonuclease; ribonuclease U₁; RNase U₁; RNase U₂; purine-specific ribonuclease; purine-specific RNase; Pleospora RNase; Trichoderma koningi RNase III; ribonuclease (purine)
References: [826, 827, 2472]

EC 3.1.27.5
Accepted name: pancreatic ribonuclease
Reaction: Endonucleolytic cleavage to nucleoside 3′-phosphates and 3′-phosphooligonucleotides ending in Cp or Up with 2′,3′-cyclic phosphate intermediates
Other name(s): RNase; RNase I; RNase A; pancreatic RNase; ribonuclease I; endoribonuclease I; ribonucleic phosphatase; alkaline ribonuclease; ribonuclease; gene S glycoproteins; Ceratitis capitata alkaline ribonuclease; SLSG glycoproteins; gene S locus-specific glycoproteins; S-genotype-asssocd. glycoproteins; ribonucleate 3′-pyrimidino-oligonucleotidohydrolase
References: [351, 158, 336]

EC 3.1.27.6
Accepted name: Enterobacter ribonuclease
Reaction: Endonucleolytic cleavage to nucleoside 3′-phosphates and 3′-phosphooligonucleotides with 2′,3′-cyclic phosphate intermediates
Comments: Preference for cleavage at CpA. Homopolymers of A, U or G are not hydrolysed.
References: [1433, 1569]

EC 3.1.27.7
Accepted name: ribonuclease F
Reaction: Endonucleolytic cleavage of RNA precursor into two, leaving 5′-hydroxy and 3′-phosphate groups
Other name(s): ribonuclease F (E. coli)
References: [893, 2756]
EC 3.1.27.8
Accepted name: ribonuclease V
Reaction: Hydrolysis of poly(A), forming oligoribonucleotides and ultimately 3′-AMP
Other name(s): endoribonuclease V
Comments: Also hydrolyses poly(U).
References: [2257]

EC 3.1.27.9
Accepted name: tRNA-intron endonuclease
Reaction: Endonucleolytic cleavage of pre-tRNA, producing 5′-hydroxy and 2′,3′-cyclic phosphate termini, and specifically removing the intron
Other name(s): transfer ribonucleate intron endoribonuclease; tRNA splicing endonuclease; splicing endonuclease; tRNATRPintron endonuclease; transfer splicing endonuclease
Comments: The enzyme catalyses the final stage in the maturation of tRNA molecules.
References: [79, 1954, 2556, 2557]

EC 3.1.27.10
Accepted name: rRNA endonuclease
Reaction: Hydrolysis of the phosphodiester linkage between guanosine and adenosine residues at one specific position in 28S rRNA from rat ribosomes
Other name(s): α-sarcin
Comments: Also acts on bacterial rRNA.
References: [630]

EC 3.1.30 Endoribonucleases that are active with either ribo- or deoxyribonucleic acids and produce 5′-phosphomonoesters

EC 3.1.30.1
Accepted name: Aspergillus nuclease S1
Reaction: Endonucleolytic cleavage to 5′-phosphomononucleotide and 5′-phosphooligonucleotide end-products
Other name(s): endonuclease S1 (Aspergillus); single-stranded-nucleate endonuclease; deoxyribonuclease S1; deoxynuclease S1; Neurospora crassa single-strand specific endonuclease; S1 nuclease; single-strand endodeoxyribonuclease; single-stranded DNA specific endonuclease; single-strand-specific endodeoxyribonuclease; single strand-specific DNase; Aspergillus oryzae S1 nuclease
References: [50, 2458, 2703]

EC 3.1.30.2
Accepted name: Serratia marcescens nuclease
Reaction: Endonucleolytic cleavage to 5′-phosphomononucleotide and 5′-phosphooligonucleotide end-products
Other name(s): endonuclease (Serratia marcescens); barley nuclease; plant nuclease I; nucleate endonuclease
Comments: Hydrolyses double- or single-stranded substrate.
References: [1656, 2424, 2425, 2764]
EC 3.1.31 Endoribonucleases that are active with either ribo- or deoxyribonucleic acids and produce 3’-phosphomonoesters

EC 3.1.31.1

Accepted name: micrococcal nuclease
Reaction: Endonucleolytic cleavage to nucleoside 3’-phosphates and 3’-phosphoholigonucleotide end-products
Other name(s): spleen endonuclease; thermonuclease; nuclease T; micrococcal endonuclease; nuclease T’; staphylococcal nuclease; spleen phosphodiesterase; *Staphylococcus aureus* nuclease; *Staphylococcus aureus* nuclease B; ribonuclease (deoxynuclease) 3’-nucleotidohydrolase
Comments: Hydrolyses double- or single-stranded substrate.
References: [28, 52, 2080, 2446]

EC 3.2 Glycosylases

This subclass contains the glycosylases, which are classified as hydrolases, although some of them can also transfer glycosyl residues to oligosaccharides, polysaccharides and other alcoholic acceptors. The glycosylases are subdivided into glycosidases, i.e., enzymes that hydrolyse O- and S-glycosyl compounds (EC 3.2.1) and those that hydrolyse N-glycosyl compounds (EC 3.2.2). Common names for enzymes acting on D-sugars or their derivatives do not normally contain ‘D’, unless ambiguity would result from the common existence of the corresponding L-sugar. Enzymes that hydrolyse a terminal, non-reducing-end glycosyl (or a well-defined di-, tri- or oligosaccharide) from a glycan, i.e. exoenzymes, are given systematic names based on ‘glycohydrolase’; enzymes that hydrolyse internal glycosidic bonds, i.e. endoenzymes, are given systematic names based on ‘glycanohydrolase’. The same structure is often used when providing accepted names for these enzymes.

EC 3.2.1 Glycosidases, i.e. enzymes that hydrolyse O- and S-glycosyl compounds

EC 3.2.1.1

Accepted name: α-amylase
Reaction: Endohydrolysis of (1→4)-α-D-glucosidic linkages in polysaccharides containing three or more (1→4)-α-linked D-glucose units
Other name(s): glycogenase; α amylase, α-amylase; endoamylase; Taka-amylase A; 1,4-α-D-glucan glucanohydrolase
Systematic name: 4-α-D-glucan glucanohydrolase
Comments: Acts on starch, glycogen and related polysaccharides and oligosaccharides in a random manner; reducing groups are liberated in the α-configuration. The term ‘α’ relates to the initial anomeric configuration of the free sugar group released and not to the configuration of the linkage hydrolysed.
References: [689, 1555, 2267]

EC 3.2.1.2

Accepted name: β-amylase
Reaction: Hydrolysis of (1→4)-α-D-glucosidic linkages in polysaccharides so as to remove successive maltose units from the non-reducing ends of the chains
Other name(s): saccharogen amylase; glycogenase; β amylase, β-amylase; 1,4-α-D-glucan maltohydrolase
Systematic name: 4-α-D-glucan maltohydrolase
Acts on starch, glycogen and related polysaccharides and oligosaccharides producing β-maltose by an inversion. The term “β” relates to the initial anomeric configuration of the free sugar group released and not to the configuration of the linkage hydrolysed.

References: [115, 723, 1555]

[EC 3.2.1.2 created 1961]

EC 3.2.1.3

Accepted name: glucan 1,4-α-glucosidase

Reaction: Hydrolysis of terminal (1→4)-linked α-D-glucose residues successively from non-reducing ends of the chains with release of β-D-glucose

Other name(s): glucoamylase; amylglucosidase; γ-amyrase; lysosomal α-glucosidase; acid maltase; exo-1,4-α-glucosidase; glucose amylase; γ,1,4-glucan glucohydrolase; acid maltase; 1,4-α-D-glucan glucohydrolase

Systematic name: 4-α-D-glucan glucohydrolase

Comments: Most forms of the enzyme can rapidly hydrolyse 1,6-α-D-glucosidic bonds when the next bond in the sequence is 1,4, and some preparations of this enzyme hydrolyse 1,6- and 1,3-α-D-glucosidic bonds in other polysaccharides. This entry covers all such enzymes acting on polysaccharides more rapidly than on oligosaccharides. EC 3.2.1.20 α-glucosidase, from mammalian intestine, can catalyse similar reactions.

References: [724, 284, 1137, 1228, 1662, 2608]

[EC 3.2.1.3 created 1961]

EC 3.2.1.4

Accepted name: cellulase

Reaction: Endohydrolysis of (1→4)-β-D-glucosidic linkages in cellulose, lichenin and cereal β-D-glucans

Other name(s): endo-1,4-β-D-glucanase; β-1,4-glucanase; β-1,4-endoglucan hydrolase; celluase A; cellulosin AP; endoglucanase D; alkali cellulase; cellulase A 3; celludextrinase; 9,5 cellulase; avicelase; pancellase SS; 1,4-(1,3;1,4)-β-D-glucan 4-glucanohydrolase

Systematic name: 4-β-D-glucan 4-glucanohydrolase

Comments: Will also hydrolyse 1,4-linkages in β-D-glucans also containing 1,3-linkages.

References: [481, 1379, 1744, 1818, 2785, 951, 952, 1093]

[EC 3.2.1.4 created 1961, modified 2001]

[3.2.1.5 Deleted entry. licheninase]

[EC 3.2.1.5 created 1961, deleted 1964]

EC 3.2.1.6

Accepted name: endo-1,3(4)-β-glucanase

Reaction: Endohydrolysis of (1→3)- or (1→4)-linkages in β-D-glucans when the glucose residue whose reducing group is involved in the linkage to be hydrolysed is itself substituted at C-3

Other name(s): endo-1,3-β-D-glucanase; laminarinase; laminaranase; β-1,3-glucanase; β-1,3,1,4-glucanase; endo-1,3-β-glucanase; endo-β-1,3(4)-glucanase; endo-β-1,3,1,4-glucanase; endo-β-(1→3)-D-glucanase; endo-1,3,1,4-β-D-glucanase; endo-β-(1-3)-D-glucanase; endo-1,3-glucanase IV; endo-1,3-β-D-glucanase; 1,3-(1,3;1,4)-β-D-glucan 3(4)-glucanohydrolase

Systematic name: 3(α or 4)-β-D-glucan 3(4)-glucanohydrolase

Comments: Substrates include laminarin, lichenin and cereal D-glucans; different from EC 3.2.1.52 β-N-acetylhexosaminidase.

References: [134, 135, 465, 2085, 2396]

[EC 3.2.1.6 created 1961, modified 1976]
EC 3.2.1.7
Accepted name: inulinase
Reaction: Endohydrolysis of (2→1)-β-D-fructosidic linkages in inulin
Other name(s): inulase; indoinulinase; endo-inulinase; exoinulinase; 2,1-β-D-fructan fructanohydrolase
Systematic name: 1-β-D-fructan fructanohydrolase
References: [17]

[EC 3.2.1.7 created 1961]

EC 3.2.1.8
Accepted name: endo-1,4-β-xylanase
Reaction: Endohydrolysis of (1→4)-β-D-xylidosidic linkages in xylans
Other name(s): endo-(1→4)-β-xylan 4-xylanohydrolase; endo-1,4-xylanase; xylanase; β-1,4-xylanase; endo-1,4-xylanase; endo-β-1,4-xylanase; endo-1,4-β-D-xylanase; 1,4-β-xylan xylanohydrolase; β-xylanase; β-1,4-xylan xylanohydrolase; endo-1,4-β-xylanase; β-D-xylanase
Systematic name: 4-β-D-xylan xylanohydrolase
References: [1049, 2784]

[EC 3.2.1.8 created 1961]

[3.2.1.9 Deleted entry. amylopectin-1,6-glucosidase]

[EC 3.2.1.9 created 1961, deleted 1972]

EC 3.2.1.10
Accepted name: oligo-1,6-glucosidase
Reaction: Hydrolysis of (1→6)-α-D-glucosidic linkages in some oligosaccharides produced from starch and glycogen by EC 3.2.1.1 (α-amylase), and in isomaltose
Other name(s): limit dextrinase (erroneous); isomaltase; sucrase-isomaltase; exo-oligo-1,6-glucosidase; dextrin 6α-glucanohydrolase; α-limit dextrinase; dextrin 6-glucanohydrolase; oligosaccharide α-1,6-glucohydrolase
Systematic name: oligosaccharide 6-α-glucohydrolase
Comments: This enzyme, like EC 3.2.1.33 (amylo-α-1,6-glucosidase), can release an α-1→6-linked glucose, whereas the shortest chain that can be released by EC 3.2.1.41 (pullulanase), EC 3.2.1.142 (limit dextrinase), and EC 3.2.1.68 (isoamylase) is maltose. It also hydrolyses isomaltulose (palatinose), isomaltotriose and panose, but has no action on glycogen or phosphorylase limit dextrin. The enzyme from intestinal mucosa is a single polypeptide chain that also catalyses the reaction of EC 3.2.1.48 (sucrose α-glucosidase). Diffsers from EC 3.2.1.33 (amylo-α-1,6-glucosidase) in its preference for short-chain substrates and in its not requiring the 6-glucosylated residue to be at a branch point, i.e. linked at both C-1 and C-4.
References: [954, 2346, 2135]

[EC 3.2.1.10 created 1961, modified 2000]

EC 3.2.1.11
Accepted name: dextranase
Reaction: Endohydrolysis of (1→6)-α-D-glucosidic linkages in dextran
Other name(s): dextran hydrolase; endodextranase; dextranase DL 2; DL 2; endo-dextranase; α-D-1,6-glucan-6-glucanohydrolase; 1,6-α-D-glucan 6-glucanohydrolase
Systematic name: 6-α-D-glucan 6-glucanohydrolase
References: [107, 529, 690, 2160]

[EC 3.2.1.11 created 1961]

[3.2.1.12 Deleted entry. cycloheptaglucanase. Now included with EC 3.2.1.54 cyclomaltodextrinase]
EC 3.2.1.14  
**Accepted name:** chitinase  
**Reaction:** Random hydrolysis of N-acetyl-β-D-glucosaminide (1→4)-β-linkages in chitin and chitodextrins  
**Other name(s):** chitodextrinase; 1,4-β-poly-N-acetylglucosaminidase; poly-β-glucosaminidase; β-1,4-poly-N-acetyl glucosaminidase; poly[1,4-(N-acetyl-β-d-glucosaminide)] glycanohydrolase  
**Systematic name:** (1→4)-2-acetamido-2-deoxy-β-D-glucan glycanohydrolase  
**Comments:** Some chitinases also display the activity defined in EC 3.2.1.17 lysozyme.  
**References:** [690, 2591, 2908]

EC 3.2.1.15  
**Accepted name:** polygalacturonase  
**Reaction:** Random hydrolysis of (1→4)-α-D-galactosiduronic linkages in pectate and other galacturanons  
**Other name(s):** pectin depolymerase; pectinase; endopolypalacturonase; pectolase; pectin hydrolase; pectin polygalacturonase; endo-polygalacturonase; poly-α-1,4-galacturonide glycanohydrolase; endogalacturonase; endo-D-galacturonase; poly(1,4-α-D-galacturonide) glycanohydrolase  
**Systematic name:** (1→4)-α-D-galacturonan glycanohydrolase  
**References:** [529, 1473, 1613, 1658, 1970]

EC 3.2.1.17  
**Accepted name:** lysozyme  
**Reaction:** Hydrolysis of (1→4)-β-linkages between N-acetylmuramic acid and N-acetyl-D-glucosamine residues in a peptidoglycan and between N-acetyl-D-glucosamine residues in chitodextrins  
**Other name(s):** muramidase; globulin G; mucopentapeptide glucohydrolase; globulin G1; N,O-diacytymuramidase; lysozyme g; L-7001; 1,4-N-acetylmuramidase; mucopentapeptide N-acetylmuramoylhydrolase; PR1-lysozyme  
**Systematic name:** peptidoglycan N-acetylmuramoylhydrolase  
**Comments:** cf. also EC 3.2.1.14 chitinase.  
**References:** [210, 213, 1155]

EC 3.2.1.18  
**Accepted name:** exo-α-sialidase  
**Reaction:** Hydrolysis of α-(2→3)-, α-(2→6)-, α-(2→8)- glycosidic linkages of terminal sialic acid residues in oligosaccharides, glycoproteins, glycolipids, colominic acid and synthetic substrates  
**Other name(s):** neuraminidase; sialidase; α-neuraminidase; acetyleneuraminidase  
**Systematic name:** acetyleneuraminyl hydrolase  
**Comments:** The enzyme does not act on 4-O-acetylated sialic acids. endo-α-Sialidase activity is listed as EC 3.2.1.129, endo-α-sialidase. See also EC 4.2.2.15 anhydrosialidase.  
**References:** [2233, 318]
EC 3.2.1.20
Accepted name: α-glucosidase
Reaction: Hydrolysis of terminal, non-reducing (1→4)-linked α-D-glucose residues with release of D-glucose
Other name(s): maltase; glucoinvertase; glucosidase; maltase-glucosaminidase; α-glucopyranosidase; glucosidinomerase; α-D-glucosidase; α-glucoside hydrolase; α-1,4-glucosidase
Systematic name: α-D-glucoside glucohydrolase
Comments: This single entry covers a group of enzymes whose specificity is directed mainly towards the exo-hydrolysis of (1→4)-α-glucosidic linkages, and that hydrolyse oligosaccharides rapidly, relative to polysaccharides, which are hydrolysed relatively slowly, or not at all. The intestinal enzyme also hydrolyses polysaccharides, catalysing the reactions of EC 3.2.1.3 glucan 1,4-α-glucosidase and, more slowly, hydrolyses (1→6)-α-D-glucose links.
References: [296, 699, 1379, 2343, 2390]

EC 3.2.1.21
Accepted name: β-glucosidase
Reaction: Hydrolysis of terminal, non-reducing β-D-glucosyl residues with release of β-D-glucose
Other name(s): gentiobiose; cellobiose; emulsin; elaterase; aryl-β-glucosidase; β-D-glucosidase; β-glucoside glucohydrolase; arbutinase; amygdalinase; p-nitrophenyl β-glucosidase; primeverosidase; amygdalase; p-rhamnase; salicilinase; β-1,6-glucohydrolase
Systematic name: β-D-glucoside glucohydrolase
Comments: Wide specificity for β-D-glucosides. Some examples also hydrolyse one or more of the following: β-D-galactosides, α-L-arabinosides, β-D-xylases, β-D-fucosides.
References: [394, 423, 471, 1003, 1379, 2199]

EC 3.2.1.22
Accepted name: α-galactosidase
Reaction: Hydrolysis of terminal, non-reducing α-D-galactose residues in α-D-galactosides, including galactose oligosaccharides, galactomannans and galactolipids
Other name(s): melibiase; α-D-galactosidase; α-galactosidase A; α-galactoside galactohydrolase
Systematic name: α-D-galactoside galactohydrolase
Comments: Also hydrolyses α-D-fucosides.
References: [2460, 2793]

EC 3.2.1.23
Accepted name: β-galactosidase
Reaction: Hydrolysis of terminal non-reducing β-D-galactose residues in β-D-galactosides
Other name(s): lactase (ambiguous); β-lactosidase; maxilact; hydrolyact; β-D-lactosidase; S 2107; lactozym; trilactase; β-D-galactanase; oryzatym; sumiklat
Systematic name: β-D-galactoside galactohydrolase
Comments: Some enzymes in this group hydrolyse α-L-arabinosides; some animal enzymes also hydrolyse β-D-fucosides and β-D-glucosides; cf. EC 3.2.1.108 lactase.
References: [214, 1337, 1350, 1375, 1489, 1695, 2725, 75]
EC 3.2.1.24

**Accepted name:** α-mannosidase

**Reaction:** Hydrolysis of terminal, non-reducing α-D-mannose residues in α-D-mannosides

**Other name(s):** α-D-mannosidase; p-nitrophenyl-α-mannosidase; α-D-mannopyranosidase; 1,2-α-mannosidase; 1,2-α-D-mannosidase; exo-α-mannosidase

**Systematic name:** α-D-mannoside mannohydrolase

**Comments:** Also hydrolyses α-D-lyxosides and heptopyranosides with the same configuration at C-2, C-3 and C-4 as mannose.

**References:** [1447, 2807]

[EC 3.2.1.24 created 1961]

EC 3.2.1.25

**Accepted name:** β-mannosidase

**Reaction:** Hydrolysis of terminal, non-reducing β-D-mannose residues in β-D-mannosides

**Other name(s):** mannanase; mannase; β-D-mannosidase; β-mannoside mannohydrolase; exo-β-D-mannanase

**Systematic name:** β-D-mannoside mannohydrolase

**References:** [17, 146, 528, 1066]

[EC 3.2.1.25 created 1961]

EC 3.2.1.26

**Accepted name:** β-fructofuranosidase

**Reaction:** Hydrolysis of terminal non-reducing β-D-fructofuranoside residues in β-D-fructofuranosides

**Other name(s):** invertase; saccharase; glucosucrase; β-h-fructosidase; β-fructosidase; invertin; sucrase; maxinvert L 1000; fructosylinvertase; alkaline invertase; acid invertase

**Systematic name:** β-D-fructofuranoside fructohydrolase

**Comments:** Substrates include sucrose; also catalyses fructotransferase reactions.

**References:** [1746, 1797]

[EC 3.2.1.26 created 1961]

[3.2.1.27 Deleted entry. α-1,3-glucosidase]

[EC 3.2.1.27 created 1961, deleted 1972]

EC 3.2.1.28

**Accepted name:** α,α-trehalase

**Reaction:** α,α-trehalose + H₂O = 2 D-glucose

**Other name(s):** trehalase

**Systematic name:** α,α-trehalose glucohydrolase

**References:** [1180, 1747]

[EC 3.2.1.28 created 1961]

[3.2.1.29 Deleted entry. chitobiase. Now included with EC 3.2.1.52, β-N-acetylhexosaminidase]

[EC 3.2.1.29 created 1961, deleted 1972]

[3.2.1.30 Deleted entry. β-D-acetylglucosaminidase. Now included with EC 3.2.1.52, β-N-acetylhexosaminidase]

[EC 3.2.1.30 created 1961, deleted 1992]
EC 3.2.1.31

Accepted name: β-glucuronidase

Reaction: a β-D-glucuronoside + H₂O = D-glucuronate + an alcohol

Other name(s): β-glucuronide glucuronohydrolase glucuronidase; exo-β-D-glucuronidase; ketodase

Systematic name: β-D-glucuronoside glucuronosohydrolase

References: [543, 574, 695, 1430, 2712]

[EC 3.2.1.31 created 1961]

EC 3.2.1.32

Accepted name: xylan endo-1,3-β-xylosidase

Reaction: Random hydrolysis of (1→3)-β-D-glycosidic linkages in (1→3)-β-D-xylans

Other name(s): xylanase; endo-1,3-β-xylanase; endo-1,3-xylanase; 1,3-β-xylanase; 1,3-β-D-xylanase; 1,3-β-D-xylan xylanohydrolase

Systematic name: 3-β-D-xylan xylanohydrolase

References: [57, 378]

[EC 3.2.1.32 created 1965]

EC 3.2.1.33

Accepted name: amylo-α-1,6-glucosidase

Reaction: Hydrolysis of (1→6)-α-D-glucosidic branch linkages in glycogen phosphorylase limit dextrin

Other name(s): amylo-1,6-glucosidase; dextrin 6-α-D-glucosidase; amylopectin 1,6-glucosidase; dextrin-1,6-glucosidase; glycogen phosphorylase-limit dextrin α-1,6-glucohydrolase

Systematic name: glycogen phosphorylase-limit dextrin 6-α-glucohydrolase

Comments: This enzyme hydrolyses an unsubstituted (1→6)-linked glucose chain. The enzyme activity found in mammals and yeast is in a polypeptide chain containing two active centres. The other activity is similar to that of EC 2.4.1.25 (4-α-glucanotransferase), which acts on the glycogen phosphorylase limit dextrin chains to expose the single glucose residues, which the 6-α-glucosidase activity can then hydrolyse. Together, these two activities constitute the glycogen debranching system.

References: [285, 1398, 1794]

[EC 3.2.1.33 created 1965, modified 2000]

[3.2.1.34 Deleted entry. chondroitinase. Now included with EC 3.2.1.35 hyaluronoglucosaminidase]

[EC 3.2.1.34 created 1965, deleted 1972]

EC 3.2.1.35

Accepted name: hyaluronoglucosaminidase

Reaction: Random hydrolysis of (1→4)-linkages between N-acetyl-β-D-glucosamine and D-glucuronate residues in hyaluronate

Other name(s): hyaluronidase; hyaluronoglucosidase; chondroitinase; chondroitinase I

Systematic name: hyaluronate 4-glycanohydrolase

Comments: Also hydrolyses 1,4-β-D-glycosidic linkages between N-acetyl-galactosamine or N-acetylgalactosamine sulfate and glucuronic acid in chondroitin, chondroitin 4- and 6-sulfates, and dermatan.

References: [1645, 2062, 2773]

[EC 3.2.1.35 created 1965, modified 1976, modified 2001 (EC 3.2.1.34 created 1965, incorporated 1972)]

EC 3.2.1.36

Accepted name: hyaluronoglucuronidase
**Reaction:** Random hydrolysis of (1→3)-linkages between β-D-glucuronate and N-acetyl-D-glucosamine residues in hyaluronate

**Other name(s):** hyaluronidase; glucuronoglucosaminoglycan hyaluronate lyase; orgelase

**Systematic name:** hyaluronate 3-glycanohydrolase

**References:** [1475, 1645]

[EC 3.2.1.36 created 1965, modified 1980]

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**EC 3.2.1.37**

**Accepted name:** xylan 1,4-β-xylosidase

**Reaction:** Hydrolysis of (1→4)-β-D-xylans, to remove successive D-xylose residues from the non-reducing termini

**Other name(s):** xylobiase; β-xylosidase; exo-1,4-β-xylosidase; β-D-xylopyranosidase; β-xylosidase; exo-1,4-β-D-xylosidase; 1,4-β-D-xylan xylohydrolase

**Systematic name:** 4-β-D-xylan xylohydrolase

**Comments:** Also hydrolyses xylobiose. Some other exoglycosidase activities have been found associated with this enzyme in sheep liver.

**References:** [394, 1049]

[EC 3.2.1.37 created 1965]

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**EC 3.2.1.38**

**Accepted name:** β-D-fucosidase

**Reaction:** Hydrolysis of terminal non-reducing β-D-fucose residues in β-D-fucosides

**Other name(s):** β-fucosidase

**Systematic name:** β-D-fucoside fucohydrolase

**Comments:** Enzymes from some sources also hydrolyse β-D-galactosides and/or β-D-glucosides and/or α-L-arabinosides. The activity of EC 3.2.1.37 xylan 1,4-β-xylosidase, is an associated activity found in some sources (e.g. liver).

**References:** [393, 394, 2136, 2794, 2795]

[EC 3.2.1.38 created 1965, deleted 1972, reinstated 1978]

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**EC 3.2.1.39**

**Accepted name:** glucan endo-1,3-β-D-glucosidase

**Reaction:** Hydrolysis of (1→3)-β-D-glucosidic linkages in (1→3)-β-D-glucans

**Other name(s):** endo-1,3-β-glucanase; laminarinase; laminaranase; oligo-1,3-glucosidase; endo-1,3-β-glucanase; callase; β-1,3-glucanase; kitalase; 1,3-β-D-glucan 3-glucanohydrolase; endo-(1,3)-β-D-glucanase; (1→3)-β-glucan 3-glucanohydrolase; endo-1,3-β-D-glucanase; endo-1,3-β-glucosidase; 1,3-β-D-glucan glucanohydrolase

**Systematic name:** 3-β-D-glucan glucanohydrolase

**Comments:** Different from EC 3.2.1.6 endo-1,3(4)-β-glucanase. Very limited action on mixed-link (1→3,1→4)-β-D-glucans. Hydrolyses laminarin, paramylon and pachyman.

**References:** [387, 2085]

[EC 3.2.1.39 created 1965]

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**EC 3.2.1.40**

**Accepted name:** α-L-rhamnosidase

**Reaction:** Hydrolysis of terminal non-reducing α-L-rhamnose residues in α-L-rhamnosides

**Other name(s):** α-L-rhamnosidase T; α-L-rhamnosidase N

**Systematic name:** α-L-rhamnose rhamnohydrolase

**References:** [2148]
EC 3.2.1.41

Accepted name: pullulanase
Reaction: Hydrolysis of (1→6)-α-D-glucosidic linkages in pullulan, amylopectin and glycogen, and in the α- and β-limit dextrins of amylopectin and glycogen
Other name(s): limit dextrinase (erroneous); amylopectin 6-glucanohydrolase; bacterial debranching enzyme; debranching enzyme; α-dextrin endo-1,6-α-glucosidase; R-enzyme; pullulan α-1,6-glucanohydrolase
Systematic name: pullulan 6-α-glucanohydrolase
Comments: Different from EC 3.2.1.142 (limit dextrinase) in its action on glycogen, and its rate of hydrolysis of limit dextrins. Its action on amylopectin is complete. Maltose is the smallest sugar that it can release from an α-(1→6)-linkage.
References: [1399, 173, 1556]

EC 3.2.1.42

Accepted name: GDP-glucosidase
Reaction: GDP-glucose + H₂O → D-glucose + GDP
Other name(s): guanosine diphosphoglucosidase; guanosine diphosphate D-glucose glucohydrolase
Systematic name: GDP-glucose glucohydrolase
References: [2387]

EC 3.2.1.43

Accepted name: β-L-rhamnosidase
Reaction: Hydrolysis of terminal, non-reducing β-L-rhamnose residues in β-L-rhamnosides
Systematic name: β-L-rhamnoside rhamnohydrolase
References: [126]

EC 3.2.1.44

Accepted name: fucoidanase
Reaction: Endohydrolysis of (1→2)-α-L-fucoside linkages in fucoidan without release of sulfate
Other name(s): α-L-fucosidase; poly(1,2-α-L-fucoside-4-sulfate) glycanohydrolase
Systematic name: poly[(1→2)-α-L-fucoside-4-sulfate] glycanohydrolase
References: [2545]

EC 3.2.1.45

Accepted name: glucosylceramidase
Reaction: D-glucosyl-N-acylsphingosine + H₂O → D-glucose + N-acylsphingosine
Other name(s): psychosine hydrolase; glucosphingosine glucosylhydrolase; GlcCer-β-glucosidase; β-D-glucocerebrosidase; glucosylcerbrosidase; β-glucosylceramidase; ceramide glucosidase; glucocerebrosidase; glucosylphosphogluconate β-glucosidase; glucosylphosphogluconate β-D-glucosidase
Systematic name: D-glucosyl-N-acylsphingosine glucohydrolase
Comments: Also acts on glucosylsphingosine (cf. EC 3.2.1.62 glycosylceramidase).
References: [253, 2655]
EC 3.2.1.46

**Accepted name:** galactosylceramidase  
**Reaction:** $\text{D-galactosyl-}N\text{-acylsphingosine} + \text{H}_2\text{O} = \text{D-galactose} + N\text{-acylsphingosine}$  
**Other name(s):** cerebroside galactosidase; galactocerebroside-β-galactosidase; galactosylcerebroside; galactocerebroside galactosidase; galactosylceramide.β-galactosidase; cerebroside β-galactosidase; galactosyleramidase I; β-galactosyleramidase; galactocerebroside-β-D-galactosidase; lactosyleramidase I; β-galactocerebiosidase; lactosyleramidase

**Systematic name:** $\text{D-galactosyl-}N\text{-acylsphingosine galactohydrolase}$  
**Comments:** cf. EC 3.2.1.62 glycosylceramidase.  
**References:** [252]

EC 3.2.1.47

**Accepted name:** galactosylgalactosyglucosylceramidase  
**Reaction:** $\text{D-galactosyl-}D\text{-galactosyl-}D\text{-glucosyl-}N\text{-acylsphingosine} + \text{H}_2\text{O} = \text{D-galactose} + \text{lactosyl-}N\text{-acylsphingosine}$  
**Other name(s):** trihexosyl ceramide galactosidase; ceramide trihexosidase; ceramidetrihexoside α-galactosidase; trihexosylceramide α-galactosidase; ceramidetrihexosidase

**Systematic name:** $\text{D-galactosyl-}D\text{-galactosyl-}D\text{-glucosyl-}N\text{-acylsphingosine galactohydrolase}$  
**References:** [251]

EC 3.2.1.48

**Accepted name:** sucrose α-glucosidase  
**Reaction:** Hydrolysis of sucrose and maltose by an α-D-glucosidase-type action  
**Other name(s):** sucrose α-glucohydrolase; sucrase; sucrase-isomaltase; sucrose.α.-glucohydrolase; intestinal sucrase; sucrase(invertase)

**Systematic name:** sucrose-α-D-glucohydrolase  
**Comments:** This enzyme is isolated from intestinal mucosa as a single polypeptide chain that also displays activity towards isomaltose (EC 3.2.1.10 oligo-1,6-glucosidase).  
**References:** [425, 954, 1301, 2324, 2346, 2502]

EC 3.2.1.49

**Accepted name:** α-N-acetylgalactosaminidase  
**Reaction:** Hydrolysis of terminal non-reducing $N$-acetyl-α-D-galactosamine residues in $N$-acetyl-α-D-galactosaminides

**Other name(s):** α-acetylgalactosaminidase; $N$-acetyl-α-D-galactosaminidase; $N$-acetyl-α-galactosaminidase  

**Systematic name:** α-N-acetyl-α-D-galactosaminide $N$-acetylgalactosaminohydrolase  
**Comments:** Splits $N$-acetylgalactosaminyl groups from O-3 of Ser and Thr.  
**References:** [2625, 2775, 2779]

EC 3.2.1.50

**Accepted name:** α-N-acetylgalactosaminidase

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Reaction: Hydrolysis of terminal non-reducing N-acetyl-D-glucosamine residues in N-acetyl-α-D-glucosaminides
Other name(s): α-acetylglucosaminidase; N-acetyl-α-D-glucosaminidase; N-acetyl-α-glucosaminidase; α-D-acetamido-2-deoxyglucosidase
Systematic name: α-N-acetyl-D-glucosaminide N-acetylglucosaminohydrolase
Comments: Hydrolyses UDP-N-acetylglucosamine.
References: [2704, 2705, 2776, 2779]

EC 3.2.1.51
Accepted name: α-L-fucosidase
Reaction: an α-L-fucoside + H₂O = L-fucose + an alcohol
Other name(s): α-fucosidase
Systematic name: α-L-fucoside fucohydrolase
References: [1431, 2088, 2512]

EC 3.2.1.52
Accepted name: β-N-acetylhexosaminidase
Reaction: Hydrolysis of terminal non-reducing N-acetyl-D-hexosamine residues in N-acetyl-β-D-hexosaminides
Other name(s): hexosaminidase; β-acetylamino deoxyhexosidase; N-acetyl-β-D-hexosaminidase; N-acetyl-β-hexosaminidase; β-hexosaminidase; β-acetylhexosaminidinase; β-D-N-acetylhexosaminidase; β-N-acetyl-β-D-hexosaminidase; β-N-acetylglucosaminidase; hexosaminidase A; N-acetylhexosaminidase; β-D-hexosaminidase
Systematic name: β-N-acetyl-D-hexosaminide N-acetylgalactosaminohydrolase
References: [317, 327, 738, 1441]

EC 3.2.1.53
Accepted name: β-N-acetylgalactosaminidase
Reaction: Hydrolysis of terminal non-reducing N-acetyl-D-galactosamine residues in N-acetyl-β-D-galactosaminides
Other name(s): N-acetyl-β-galactosaminidase; N-acetyl-β-D-galactosaminidase; β-acetylgalactosaminidase; β-D-N-acetylgalactosaminidase; N-acetylgalactosaminidase
Systematic name: β-N-acetyl-D-galactosaminide N-acetylgalactosaminohydrolase
References: [738, 1034]

EC 3.2.1.54
Accepted name: cyclomaltodextrinase
Reaction: cyclomaltodextrin + H₂O = linear maltodextrin
Other name(s): cycloheptaglucanase; cyclohexaglucanase; cyclodextrinase
Systematic name: cyclomaltodextrin dextrin-hydrolase (decyclizing)
Comments: Also hydrolyses linear maltodextrin.
References: [522]
EC 3.2.1.55
Accepted name: α-N-arabinofuranosidase
Reaction: Hydrolysis of terminal non-reducing α-L-arabinofuranoside residues in α-L-arabinosides
Other name(s): arabinosidase; α-arabinosidase; α-L-arabinosidase; α-arabinofuranosidase; polysaccharide α-L-arabinofuranosidase; α-L-arabinofuranoside hydrolase; L-arabinosidase; α-L-arabinanase
Systematic name: α-L-arabinofuranosidase arabinofuranohydrolase
Comments: The enzyme acts on α-L-arabinofuranosides, α-L-arabinans containing (1,3)- and/or (1,5)-linkages, arabinoxylans and arabinogalactans. Some β-galactosidases (EC 3.2.1.23) and β-D-fucosidases (EC 3.2.1.38) also hydrolyse α-L-arabinosides.
References: [1176, 1177, 2475]

[EC 3.2.1.55 created 1972, modified 1976 (EC 3.2.1.79 created 1972, incorporated 1976)]

EC 3.2.1.56
Accepted name: glucuronosyl-disulfoglucosamine glucuronidase
Reaction: 3-D-glucuronosyl-N²,6-disulfo-β-D-glucosamine + H₂O = d-glucuronate + N²,6-disulfo-D-glucosamine
Other name(s): glycuronidase; 3-D-glucuronsyl-2-N²,6-disulfo-β-D-glucosamine glucuronohydrolase
Systematic name: 3-D-glucuronsyl-N²,6-disulfo-β-D-glucosamine glucuronohydrolase
References: [540]

[EC 3.2.1.56 created 1972]

EC 3.2.1.57
Accepted name: isopullulanase
Reaction: Hydrolysis of pullulan to isopanose (6-α-maltosylglucose)
Systematic name: pullulan 4-glucanohydrolase (isopanose-forming)
Comments: The enzyme has practically no action on starch. Panose (4-α-isomaltosylglucose) is hydrolysed to isomaltose and glucose. cf. EC 3.2.1.41 (pullulanase) and EC 3.2.1.135 (neopullulanase).
References: [2188]

[EC 3.2.1.57 created 1972]

EC 3.2.1.58
Accepted name: glucan 1,3-α-glucosidase
Reaction: Successive hydrolysis of β-D-glucose units from the non-reducing ends of (1→3)-β-D-glucans, releasing α-glucose
Other name(s): exo-1,3-β-glucosidase; β-1,3-glucan exo-hydrolase; exo (1→3)-glucanohydrolase; 1,3-β-glucan glucohydrolase
Systematic name: 3-β-D-glucan glucohydrolase
Comments: Acts on oligosaccharides, but very slowly on laminaribiose.
References: [134, 135]

[EC 3.2.1.58 created 1972]

EC 3.2.1.59
Accepted name: glucan endo-1,3-α-glucosidase
Reaction: Endohydrolysis of (1→3)-α-D-glucosidic linkages in isolichenin, pseudonigeran and nigeran
Other name(s): endo-1,3-α-glucanase; mutanase; endo-(1→3)-α-glucanase; cariogenase; cariogenanase; endo-1,3-α-D-glucanase; 1,3(1,3;1,4)-α-D-glucan 3-glucanohydrolase
Systematic name: 3-α-D-glucan 3-glucanohydrolase
Comments: Products from pseudonigeran (1,3-α-D-glucan) are nigerose and α-D-glucose.
References: [942]

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EC 3.2.1.60

Accepted name: glucan 1,4-α-maltotetrahydrolase
Reaction: Hydrolysis of (1→4)-α-D-glucosidic linkages in amylaceous polysaccharides, to remove successive maltotetraose residues from the non-reducing chain ends
Other name(s): exo-maltotetrahydrolase; 1,4-α-D-glucan maltotetrahydrolase
Systematic name: 4-α-D-glucan maltotetrahydrolase
Comments: Compare EC 3.2.1.2 β-amylase, which removes successive maltose residues, and EC 3.2.1.98 (glucan 1,4-α-maltohexaosidase) and EC 3.2.1.116 (glucan 1,4-α-maltotriohydrolase).
References: [1773, 2130]

EC 3.2.1.61

Accepted name: mycodextranase
Reaction: Endohydrolysis of (1→4)-α-D-glucosidic linkages in α-D-glucans containing both (1→3)- and (1→4)-bonds
Other name(s): 1,3,1,4-α-D-glucan 4-glucanohydrolase
Systematic name: (1→3)-(1→4)-α-D-glucan 4-glucanohydrolase
Comments: Products are nigerose and 4-α-D-nigerosylglucose. No hydrolysis of α-D-glucans containing only 1,3- or 1,4-bonds.
References: [2624]

EC 3.2.1.62

Accepted name: glycosylceramidase
Reaction: glycosyl-N-acylsphingosine + H₂O = N-acylsphingosine + a sugar
Other name(s): phlorizin hydrolase; phloretin-glucosidase; glycosyl ceramide glycosylhydrolase; cerebrosidase; phloridzin β-glucosidase; lactase-phlorizin hydrolase; phloridzin glucosidase
Systematic name: glycosyl-N-acylsphingosine glycohydrolase
Comments: Broad specificity [cf. EC 3.2.1.45 (glucosylceramidase) and EC 3.2.1.46 (galactosylceramidase)]. Also hydrolysse phlorizin to phloretin and glucose. The intestinal enzyme is a complex that also catalyses the reaction of EC 3.2.1.108 lactase.
References: [1414, 1496, 1543]

EC 3.2.1.63

Accepted name: 1,2-α-L-fucosidase
Reaction: methyl-2-α-L-fucopyranosyl-β-D-galactoside + H₂O = L-fucose + methyl β-D-galactoside
Other name(s): almond emulsin fucosidase; α-(1→2)-L-fucosidase
Systematic name: 2-α-L-fucopyranosyl-β-D-galactoside fucohydrolase
Comments: Highly specific for non-reducing terminal L-fucose residues linked to D-galactose residues by a 1,2-α-linkage. Not identical with EC 3.2.1.111 1,3-α-L-fucosidase.
References: [104, 1863, 2088]

EC 3.2.1.64

Accepted name: 2,6-β-fructan 6-levanbiohydrolase
Reaction: Hydrolysis of (2→6)-β-D-fructofuranan, to remove successive disaccharide residues as levanbiose, i.e. 6-(β-D-fructofuranosyl)-D-fructose, from the end of the chain

Other name(s): β-2,6-fructan-6-levanbiohydrolase; 2,6-β-D-fructan 6-levanbiohydrolase; levanbiose-producing levananase; 2,6-β-D-fructan 6-β-D-fructofuranosylfructohydrolase

Systematic name: (2→6)-β-D-fructofuranan 6-β-D-fructofuranosylfructohydrolase

References: [91, 2183, 2184, 2382, 1198]

[EC 3.2.1.64 created 1972, modified 2004]

EC 3.2.1.65

Accepted name: levanase

Reaction: Random hydrolysis of (2→6)-β-D-fructofuranosidic linkages in (2→6)-β-D-fructans (levans) containing more than 3 fructose units

Other name(s): levan hydrolase; 2,6-β-D-fructan fructohydrolase

Systematic name: (2→6)-β-D-fructan fructohydrolase

References: [90]

[EC 3.2.1.65 created 1972]

EC 3.2.1.66

Accepted name: quercitrinase

Reaction: quercitrin + H₂O = L-rhamnose + quercetin

Systematic name: quercitrin 3-L-rhamnohydrolase

Comments: Quercitrin is quercetin 3-L-rhamnoside.

References: [2780]

[EC 3.2.1.66 created 1972]

EC 3.2.1.67

Accepted name: galacturan 1,4-α-galacturonidase

Reaction: [(1→4)-α-D-galacturonide]ₙ + H₂O = [(1→4)-α-D-galacturonide]ₙ₋₁ + D-galacturonate

Other name(s): exopolygalacturonase; poly(galacturonate) hydrolase; exo-D-galacturonase; exo-D-galacturonanase; exopoly-D-galacturonase; poly(1,4-α-D-galacturonide) galacturonohydrolase

Systematic name: poly[(1→4)-α-D-galacturonide] galacturonohydrolase

References: [941]

[EC 3.2.1.67 created 1972]

EC 3.2.1.68

Accepted name: isoamylase

Reaction: Hydrolysis of (1→6)-α-D-glucosidic branch linkages in glycogen, amylopectin and their β-limit dextrans

Other name(s): debranching enzyme; glycogen α-1,6-glucanohydrolase

Systematic name: glycogen 6-α-D-glucanohydrolase

Comments: Also readily hydrolyses amylopectin. Differs from EC 3.2.1.41 (pullulanase) and EC 3.2.1.142 (limit dextrinase) by its inability to hydrolyse pullulan, and by limited action on α-limit dextrans. Maltose is the smallest sugar it can release from an α-(1→6)-linkage.

References: [2883]

[EC 3.2.1.68 created 1972, modified 1976, modified 2000]

[3.2.1.69 Deleted entry. amylopectin 6-glucanohydrolase. Now included with EC 3.2.1.41 pullulanase]

[EC 3.2.1.69 created 1972, deleted 1976]
EC 3.2.1.70
Accepted name: glucan 1,6-α-glucosidase
Reaction: Hydrolysis of (1→6)-α-D-glucosidic linkages in (1→6)-α-D-glucans and derived oligosaccharides
Other name(s): exo-1,6-β-glucosidase; glucodextrinase; glucan α-1,6-D-glucohydrolase
Systematic name: glucan 6-α-D-glucohydrolase
Comments: Hydrolysis is accompanied by inversion at C-1, so that new reducing ends are released in the β-configuration. Dextrans and isomaltosaccharides are hydrolysed, as is isomaltose, but very slowly. The enzyme from some sources also possesses the activity of EC 3.2.1.59 (glucan endo-1,3-α-glucosidase).
References: [1888, 2223, 2721]

[EC 3.2.1.70 created 1972, modified 2001]

EC 3.2.1.71
Accepted name: glucan endo-1,2-β-glucosidase
Reaction: Random hydrolysis of (1→2)-glucosidic linkages in (1→2)-β-D-glucans
Other name(s): endo-1,2-β-glucanase; β-D-1,2-glucanase; endo-(1→2)-β-D-glucanase; 1,2-β-D-glucan glucanohydrolase
Systematic name: 2-β-D-glucan glucanohydrolase
References: [2086]

[EC 3.2.1.71 created 1972]

EC 3.2.1.72
Accepted name: xylan 1,3-β-xylosidase
Reaction: Hydrolysis of successive xylose residues from the non-reducing termini of (1→3)-β-D-xylans
Other name(s): 1,3-β-xylosidase, exo-1,3-β-xylosidase; β-1,3'-xylanase; exo-β-1,3'-xylanase; 1,3-β-D-xylan xylohydrolase
Systematic name: 3-β-D-xylan xylohydrolase
References: [764]

[EC 3.2.1.72 created 1972]

EC 3.2.1.73
Accepted name: licheninase
Reaction: Hydrolysis of (1→4)-β-D-glucosidic linkages in β-D-glucans containing (1→3)- and (1→4)-bonds
Other name(s): lichenase; β-(1→4)-D-glucan 4-glucanohydrolase; 1,3;1,4-β-glucan endohydrolase; 1,3;1,4-β-glucan 4-glucanohydrolase; 1,3,1,4-β-D-glucan 4-glucanohydrolase
Systematic name: (1→3)-(1→4)-β-D-glucan 4-glucanohydrolase
Comments: Acts on lichenin and cereal β-D-glucans, but not on β-D-glucans containing only 1,3- or 1,4-bonds.
References: [133]

[EC 3.2.1.73 created 1972]

EC 3.2.1.74
Accepted name: glucan 1,4-β-glucosidase
Reaction: Hydrolysis of (1→4)-linkages in (1→4)-β-D-glucans, to remove successive glucose units
Other name(s): exo-1,4-β-glucosidase; exocellulase; exo-β-1,4-glucosidase; exo-β-1,4-glucanase; β-1,4-β-glucanase; β-glucosidase; exo-1,4-β-glucanase; 1,4-β-D-glucan glucohydrolase
Systematic name: 4-β-D-glucan glucohydrolase
Comments: Acts on 1,4-β-D-glucans and related oligosaccharides. Cellobiose is hydrolysed, but very slowly.
References: [133]
EC 3.2.1.74

**Accepted name:** glucan endo-1,6-β-glucosidase  
**Reaction:** Random hydrolysis of (1→6)-linkages in (1→6)-β-D-glucans  
**Other name(s):** endo-1,6-β-glucanase; β-1→6-β-D-glucanase; β-1,6-glucanase-pustulanase; β-1,6-glucan hydrolase; β-1,6-glucan 6-glucanohydrolase; 1,6-β-D-glucan glucanohydrolase  
**Systematic name:** 6-β-D-glucan glucanohydrolase  
**Comments:** Acts on lutean, pustulan and 1,6-oligo-β-D-glucosides.  
**References:** [2087]

EC 3.2.1.75

**Accepted name:** glucan endo-1,6-β-glucosidase  
**Reaction:** Random hydrolysis of (1→6)-linkages in (1→6)-β-D-glucans  
**Other name(s):** endo-1,6-β-glucanase; β-1→6-β-D-glucanase; β-1,6-glucanase-pustulanase; β-1,6-glucan hydrolase; β-1,6-glucan 6-glucanohydrolase; 1,6-β-D-glucan glucanohydrolase  
**Systematic name:** 6-β-D-glucan glucanohydrolase  
**Comments:** Acts on lutean, pustulan and 1,6-oligo-β-D-glucosides.  
**References:** [2087]

EC 3.2.1.76

**Accepted name:** L-iduronidase  
**Reaction:** Hydrolysis of unsulfated α-L-iduronosidic linkages in dermatan sulfate  
**Other name(s):** α-L-iduronidase  
**Systematic name:** glycosaminoglycan α-L-iduronohydrolase  
**References:** [1587, 2141, 2409]

EC 3.2.1.77

**Accepted name:** mannan 1,2-(1,3)-α-mannosidase  
**Reaction:** Hydrolysis of (1→2)- and (1→3)-linkages in yeast mannan, releasing mannose  
**Other name(s):** exo-1,2,1,3-α-mannosidase; 1,2,1,3-α-D-mannan mannohydrolase  
**Systematic name:** (1→2)-(1→3)-α-D-mannan mannohydrolase  
**Comments:** A 1,6-α-D-mannan backbone remains after action on yeast mannan. This is further attacked, but slowly.  
**References:** [1157, 1158]

EC 3.2.1.78

**Accepted name:** mannan endo-1,4-β-mannosidase  
**Reaction:** Random hydrolysis of (1→4)-β-D-mannosidic linkages in mannans, galactomannans and glucomannans  
**Other name(s):** endo-1,4-β-mannanase; endo-β-1,4-mannanase; β-mannanase B; β-1, 4-mannan 4-mannanohydrolase; endo-β-mannanase; β-D-mannanase; 1,4-β-D-mannan mannanohydrolase  
**Systematic name:** 4-β-D-mannan mannanohydrolase  
**References:** [637, 2084]

EC 3.2.1.79

Deleted entry. α-L-arabinofuranoside hydrolase. Now included with EC 3.2.1.55 α-N-arabinofuranosidase

EC 3.2.1.80

**Accepted name:** fructan β-fructosidase  
**Reaction:** Hydrolysis of terminal, non-reducing (2→1)- and (2→6)-linked β-D-fructofuranose residues in fructans  
**Other name(s):** exo-β-D-fructosidase; exo-β-fructosidase; polysaccharide β-fructofuranosidase; fructan exohydrolase
**Systematic name:** \(\beta\)-D-fructan fructohydrolase  
**Comments:** Hydrolyses inulin and levan, and also sucrose.  
**References:** [468, 1118]  

[EC 3.2.1.80 created 1972]

**EC 3.2.1.81**  
**Accepted name:** \(\beta\)-agarase  
**Reaction:** Hydrolysis of \((1\rightarrow4)\)-\(\beta\)-D-galactosidic linkages in agarose, giving the tetramer as the predominant product  
**Other name(s):** agarase (ambiguous); AgaA; AgaB; endo-\(\beta\)-agarase; agarose 3-glycanohydrolase (incorrect)  
**Systematic name:** agarose 4-glycanohydrolase  
**Comments:** Also acts on porphyran, but more slowly [588]. This enzyme cleaves the \(\beta-(1\rightarrow4)\) linkages of agarose in a random manner with retention of the anomeric-bond configuration, producing \(\beta\)-anomers that give rise progressively to \(\alpha\)-anomers when mutarotation takes place [1129]. The end products of hydrolysis are neoagarotetraose and neoagarohexaose in the case of AgaA from the marine bacterium *Zobellia galactanivorans*, and neoagarotetraose and neoagarobiose in the case of AgaB [1129].  
**References:** [588, 35, 1884, 1883, 2440, 1129]  

[EC 3.2.1.81 created 1972, modified 2006]

**EC 3.2.1.82**  
**Accepted name:** exo-poly-\(\alpha\)-galacturonosidase  
**Reaction:** Hydrolysis of pectic acid from the non-reducing end, releasing digalacturonate  
**Other name(s):** exopolygalacturonosidase; exopolygalacturanosidase; poly(1,4-\(\alpha\)-D-galactosiduronate) digalacturonohydrolase  
**Systematic name:** poly[(1\rightarrow4)-\(\alpha\)-D-galactosiduronate] digalacturonohydrolase  
**References:** [941, 949, 950]  

[EC 3.2.1.82 created 1972]

**EC 3.2.1.83**  
**Accepted name:** \(\kappa\)-carrageenase  
**Reaction:** Endohydrolysis of \((1\rightarrow4)\)-\(\beta\)-D-linkages between D-galactose 4-sulfate and 3,6-anhydro-D-galactose in \(\kappa\)-carrageenans  
**Other name(s):** \(\kappa\)-carrageenan 4-\(\beta\)-D-glycanohydrolase  
**Systematic name:** \(\kappa\)-carrageenan 4-\(\beta\)-D-glycanohydrolase (configuration-retaining)  
**Comments:** The main products of hydrolysis are neocarrabiose-sulfate and neocarratetraose-sulfate [1651]. Unlike EC 3.2.1.157 (\(\iota\)-carrageenase), but similar to EC 3.2.1.81 (\(\beta\)-agarase), this enzyme proceeds with retention of the anomeric configuration.  
**References:** [2769, 2013, 2011, 1650, 1651]  

[EC 3.2.1.83 created 1972, modified 2006]

**EC 3.2.1.84**  
**Accepted name:** glucan 1,3-\(\alpha\)-glucosidase  
**Reaction:** Hydrolysis of terminal \((1\rightarrow3)\)-\(\alpha\)-D-glucosidic links in \((1\rightarrow3)\)-\(\alpha\)-D-glucans  
**Other name(s):** exo-1,3-\(\alpha\)-glucanase; glucosidase II; 1,3-\(\alpha\)-D-glucan 3-glucohydrolase  
**Systematic name:** 3-\(\alpha\)-D-glucan 3-glucohydrolase  
**Comments:** Does not act on nigeran.  
**References:** [2927]  

[EC 3.2.1.84 created 1972]
EC 3.2.1.85

Accepted name: 6-phospho-β-galactosidase
Reaction: a 6-phospho-β-D-galactoside + H₂O = 6-phospho-D-galactose + an alcohol
Other name(s): phospho-β-galactosidase; β-D-phosphogalactoside galactohydrolase; phospho-β-D-galactosidase; 6-phospho-β-D-galactosidase
Systematic name: 6-phospho-β-D-galactoside 6-phosphogalactohydrolase
References: [981]

[EC 3.2.1.85 created 1976]

EC 3.2.1.86

Accepted name: 6-phospho-β-glucosidase
Reaction: 6-phospho-β-D-glucosyl-(1→4)-D-glucose + H₂O = D-glucose + D-glucose 6-phosphate
Other name(s): phospho-β-glucosidase A; phospho-β-glucosidase; phosphocellobiase; 6-phospho-β-D-glucosyl-(1,4)-D-glucose glucohydrolase
Systematic name: 6-phospho-β-D-glucosyl-(1→4)-D-glucose glucohydrolase
Comments: Also hydrolyses several other phospho-β-D-glucosides, but not their non-phosphorylated forms.
References: [1934]

[EC 3.2.1.86 created 1976]

EC 3.2.1.87

Accepted name: capsular-polysaccharide endo-1,3-α-galactosidase
Reaction: Random hydrolysis of (1→3)-α-D-galactosidic linkages in Aerobacter aerogenes capsular polysaccharide
Other name(s): polysaccharide depolymerase; capsular polysaccharide galactohydrolase
Systematic name: Aerobacter-capsular-polysaccharide galactohydrolase
Comments: Hydrolyses the galactosyl-α-1,3-D-galactose linkages only in the complex substrate, bringing about depolymerization.
References: [2901, 2902]

[EC 3.2.1.87 created 1976]

EC 3.2.1.88

Accepted name: β-L-arabinosidase
Reaction: a β-L-arabinoside + H₂O = L-arabinose + an alcohol
Other name(s): vicianosidase
Systematic name: β-L-arabinoside arabinohydrolase
References: [534]

[EC 3.2.1.88 created 1976]

EC 3.2.1.89

Accepted name: arabinogalactan endo-1,4-β-galactosidase
Reaction: Endohydrolysis of (1→4)-β-D-galactosidic linkages in arabinogalactans
Other name(s): endo-1,4-β-galactanase; galactanase; arabinogalactanase
Systematic name: arabinogalactan 4-β-D-galactanohydrolase
References: [624, 1370]

[EC 3.2.1.89 created 1976]

[3.2.1.90 Deleted entry. arabinogalactan endo-1,3-β-galactosidase. The enzyme was not sufficiently characterized to warrant an EC number]

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EC 3.2.1.91

Accepted name: cellulose 1,4-β-cellobiosidase
Reaction: Hydrolysis of (1→4)-β-D-glucosidic linkages in cellulose and cellotetraose, releasing cellobiose from the non-reducing ends of the chains
Other name(s): exo-cellobiohydrolase; β-1,4-glucan cellobiohydrolase; β-1,4-glucan cellobiosylhydrolase; 1,4-β-glucan cellobiosidase; exoglucanase; avicelase; CBH I; C1 cellulase; cellobiohydrolase I; cellobiohydrolase; exo-β-1,4-glucan cellobiohydrolase; 1,4-β-D-glucan cellobiohydrolase; cellobiosidase
Systematic name: 4-β-D-glucan cellobiohydrolase
References: [175, 638, 911]

EC 3.2.1.92

Accepted name: peptidoglycan β-N-acetylmuramidase
Reaction: Hydrolysis of terminal, non-reducing N-acetylmuramic residues
Other name(s): exo-β-N-acetylmuramidase; exo-β-acetylmuramidase; β-2-acetamido-3-O-(D-1-carboxyethyl)-2-deoxy-D-glucoside acetamidodeoxyglucohydrolase
Systematic name: peptidoglycan β-N-acetylmuramoylhexohydrolase
References: [2114]

EC 3.2.1.93

Accepted name: α,α-phosphotrehalase
Reaction: α,α-trehalose 6-phosphate + H2O = D-glucose + D-glucose 6-phosphate
Other name(s): phosphotrehalase
Systematic name: α,α-trehalose-6-phosphate phosphoglucohydrolase
References: [190]

EC 3.2.1.94

Accepted name: glucan 1,6-α-isomaltosidase
Reaction: Hydrolysis of (1→6)-α-D-glucosidic linkages in polysaccharides, to remove successive isomaltose units from the non-reducing ends of the chains
Other name(s): exo-isomaltohydrolase; isomalto-dextranase; isomaltodextranase; G2-dextranase; 1,6-α-D-glucan isomaltohydrolase
Systematic name: 6-α-D-glucan isomaltohydrolase
Comments: Optimum activity is on those 1,6-α-D-glucans containing 6, 7 and 8 glucose units; those containing 3, 4 and 5 glucose units are hydrolysed at slower rates.
References: [2222, 2221]

EC 3.2.1.95

Accepted name: dextran 1,6-α-isomaltotriosidase
Reaction: Hydrolysis of (1→6)-α-D-glucosidic linkages in dextrans, to remove successive isomaltotriose units from the non-reducing ends of the chains
Other name(s): exo-isomaltotriohydrolase; 1,6-α-D-glucan isomaltotriohydrolase
Systematic name: 6-α-D-glucan isomaltotriohydrolase
References: [2443]
EC 3.2.1.96

**Accepted name:** mannosyl-glycoprotein endo-β-N-acetylglicosaminidase

**Reaction:** Endohydrolysis of the \(N,N'\)-diacetylchitobiosyl unit in high-mannose glycopeptides and glycoproteins containing the \{-Man(GlcNAc)\}_2\text{Asn}- structure. One \(N\)-acetyl-D-glucosamine residue remains attached to the protein; the rest of the oligosaccharide is released intact

**Other name(s):** \(N,N'\)-diacetylchitobiosyl \(β\)-\(N\)-acetylglicosaminidase; endo-\(β\)-\(N\)-acetylglicosaminidase; mannosyl-glycoprotein endo-\(β\)-\(N\)-acetylglicosaminidase; di-\(N\)-acetylchitobiosyl \(β\)-\(N\)-acetylglicosaminidase; endo-\(β\)-\(N\)-acetylglicosaminidase; endo-\(β\)-(1→4)-\(N\)-acetylglicosaminidase; mannosyl-glycoprotein 1,4-\(N\)-acetamido-\(β\)-\(D\)-glycohydrolase; endoglycosidase S; endo-\(β\)-\(N\)-acetylglicosaminidase F; endo-\(β\)-\(N\)-acetylglicosaminidase H; endo-\(β\)-\(N\)-acetylglicosaminidase D; endo-\(β\)-\(N\)-acetylglicosaminidase L; glycopeptide-\(d\)-mannosyl-4-(\(N\)-acetyl-\(D\)-glucosaminyl)\_2-asparagine 1,4-\(N\)-acetyl-\(β\)-glucosaminohydrolase; endoglycosidase H

**Systematic name:** glycopeptide-\(d\)-mannosyl-\(N^4\)-(\(N\)-acetyl-\(D\)-glucosaminyl)\_2-asparagine 1,4-\(N\)-acetyl-\(β\)-glucosaminohydrolase

**Comments:** A group of related enzymes.

**References:** [390, 1299, 1975, 1976, 2477, 2529]

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EC 3.2.1.97

**Accepted name:** glycopeptide \(α\)-\(N\)-acetylgalactosaminidase

**Reaction:** Hydrolysis of \(O\)-glycosidic linkages of sugar chains between \(α\)-\(N\)-acetyl-\(D\)-galactosamine and serine or threonine residues in glycoproteins

**Other name(s):** endo-\(α\)-\(N\)-acetylgalactosaminidase; endo-\(α\)-\(N\)-acetyl-\(D\)-galactosaminidase; mucinaminylserine mucinaminidase; \(D\)-galactosyl-3-(\(N\)-acetyl-\(α\)-\(D\)-galactosaminyl)-L-serine mucinaminohydrolase; endo-\(α\)-GalNAc-ase

**Systematic name:** \(D\)-galactosyl-\(N\)-acetyl-\(α\)-\(D\)-galactosamine \(D\)-galactosyl-\(N\)-acetyl-galactosaminohydrolase

**Comments:** The inability of the enzyme to hydrolyse substrates such as NeuAc→Gal→GalNAc-Ser/Thr, GalNAc→Gal→GalNAc→Ser/Thr, GalNAc→(Fuc)→GalNAc-Ser/Thr and NeuAc→GalNAc-Ser/Thr, together with the fact that galactose is an inhibitor of the enzyme, suggests that a non-reducing galactose terminus is necessary for recognition of the substrate by the enzyme [2639]. The enzyme cannot release Gal→GalNAc from asialo (GM1) ganglioside, which suggests that the \(β\)-\(N\)-acetylgalactosaminyl linkage is not recognized by the enzyme [2639].

**References:** [189, 629, 2639]

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EC 3.2.1.98

**Accepted name:** glucan 1,4-\(α\)-maltohexaosidase

**Reaction:** Hydrolysis of (1→4)-\(α\)-\(D\)-glucosidic linkages in amylaceous polysaccharides, to remove successive maltohexaose residues from the non-reducing chain ends

**Other name(s):** exo-maltohexaohydrolase; 1,4-\(α\)-\(D\)-glucan maltohexaohydrolase

**Systematic name:** 4-\(α\)-\(D\)-glucan maltohexaohydrolase

**Comments:** cf. EC 3.2.1.3 glucan 1,4-\(α\)-glucosidase, which removes successive glucose residues; EC 3.2.1.2 \(β\)-amylase, which removes successive maltose residues; EC 3.2.1.116 glucan 1,4-\(α\)-maltotriohydrolase, which removes successive maltotriose units and EC 3.2.1.60 glucan 1,4-\(α\)-maltotetrahydrodrolase, which removes successive maltotetraose residues. The products have the \(α\)-configuration.

**References:** [1174, 1773]
EC 3.2.1.99
Accepted name: arabinan endo-1,5-α-L-arabinosidase
Reaction: Endohydrolysis of (1→5)-α-arabinofuranosidic linkages in (1→5)-arabinans
Other name(s): endo-1,5-α-L-arabinanase; endo-α-1,5-arabanase; endo-arabanase; 1,5-α-L-arabinan 1,5-α-L-arabinanohydrolase
Systematic name: 5-α-L-arabinan 5-α-L-arabinanohydrolase
Comments: Also acts on beet arabinan, but more slowly.
References: [1175, 2772]

[EC 3.2.1.99 created 1981]

EC 3.2.1.100
Accepted name: mannan 1,4-mannobiosidase
Reaction: Hydrolysis of (1→4)-β-D-mannosidic linkages in (1→4)-β-D-mannans, to remove successive manno-bose residues from the non-reducing chain ends
Other name(s): 1,4-β-D-mannan mannobiohydrolase; exo-β-mannanase; exo-1,4-β-mannobiohydrolase
Systematic name: 4-β-D-mannan mannobiohydrolase
References: [61]

[EC 3.2.1.100 created 1983]

EC 3.2.1.101
Accepted name: mannan endo-1,6-α-mannosidase
Reaction: Random hydrolysis of (1→6)-α-D-mannosidic linkages in unbranched (1→6)-mannans
Other name(s): exo-1,6-β-mannanase; endo-α-1→6-D-mannanase; endo-1,6-β-mannanase; mannan endo-1,6-β-mannosidase; 1,6-α-D-mannan mannanohydrolase
Systematic name: 6-α-D-mannan mannanohydrolase
References: [1771, 266, 1770]

[EC 3.2.1.101 created 1984, modified 2001]

EC 3.2.1.102
Accepted name: blood-group-substance endo-1,4-β-galactosidase
Reaction: Endohydrolysis of (1→4)-β-D-galactosidic linkages in blood group A and B substances
Other name(s): endo-β-galactosidase; blood-group-substance 1,4-β-D-galactanohydrolase
Systematic name: blood-group-substance 4-β-D-galactanohydrolase
Comments: Hydrolyses the 1,4-β-D-galactosyl linkages adjacent to a 1,3-α-D-galactosyl or N-acetylgalactosaminyl residues and a 1,2-α-D-fucosyl residue.
References: [763, 1780, 2496]

[EC 3.2.1.102 created 1984]

EC 3.2.1.103
Accepted name: keratan-sulfate endo-1,4-β-galactosidase
Reaction: Endohydrolysis of (1→4)-β-D-galactosidic linkages in keratan sulfate
Other name(s): endo-β-galactosidase; keratan sulfate endogalactosidase; keratanase; keratan-sulfate 1,4-β-D-galactanohydrolase
Systematic name: keratan-sulfate 4-β-D-galactanohydrolase
Comments: Hydrolyses the 1,4-β-D-galactosyl linkages adjacent to 1,3-α-D-N-acetyl-glucosaminyl residues. Also acts on some non-sulfated oligosaccharides, but only acts on blood group substances when the 1,2-linked fucosyl residues have been removed (cf. EC 3.2.1.102 blood-group-substance endo-1,4-β-galactosidase).
References: [763]
EC 3.2.1.104

Accepted name: steryl-β-glucosidase
Reaction: cholesteryl-β-D-glucoside + H₂O = D-glucose + cholesterol
Systematic name: cholesteryl-β-D-glucoside glucohydrolase
Comments: Acts on glucosides of cholesterol and sitosterol, but not on some related sterols such as coprostanol.
References: [1181]

EC 3.2.1.105

Accepted name: 3α(S)-strictosidine β-glucosidase
Reaction: strictosidine + H₂O = D-glucose + strictosidine aglycone
Systematic name: strictosidine β-D-glucohydrolase
Comments: Does not act on a number of closely related glycosides. Strictosidine is a precursor of indole alkaloids.
References: [978, 128]

EC 3.2.1.106

Accepted name: mannosyl-oligosaccharide glucosidase
Reaction: Exohydrolysis of the non-reducing terminal glucose residues in the mannosyl-oligosaccharide Glc₃Man₉GlcNAc₂
Other name(s): Glc₃Man₉NAc₂ oligosaccharide glucosidase; trimming glucosidase I
Systematic name: mannosyl-oligosaccharide glucohydrolase
Comments: Also acts, more slowly, on the corresponding glycolipids and glycopeptides. Involved in the formation of high-mannose and complex glycoproteins.
References: [621, 871, 1252, 872, 1565]

EC 3.2.1.107

Accepted name: protein-glucosylgalactosylhydroxylysine glucosidase
Reaction: protein α-D-glucosyl-(1→2)-β-D-galactosyl-L-hydroxylysine + H₂O = D-glucose + protein β-D-galactosyl-L-hydroxylysine
Other name(s): 2-O-α-D-glucopyranosyl-5-O-α-D-galactopyranosylhydroxy-L-lysine glucohydrolase; protein-α-D-glucosyl-1,2-β-D-galactosyl-L-hydroxylysine glucohydrolase
Systematic name: protein-α-D-glucosyl-(1→2)-β-D-galactosyl-L-hydroxylysine glucohydrolase
Comments: Requires free, positively charged ε-amino group of hydroxylysine.
References: [914, 915, 2423]

EC 3.2.1.108

Accepted name: lactase
Reaction: lactose + H₂O = D-galactose + D-glucose
Other name(s): lactase-phlorizin hydrolase
Systematic name: lactose galactohydrolase
Comments: The enzyme from intestinal mucosa is isolated as a complex that also catalyses the reaction of EC 3.2.1.62 glycosylceramidase. cf. EC 3.2.1.33 amylo-α-1,6-glucosidase.
References: [1496, 2050, 2244, 2355, 2356, 75]
EC 3.2.1.108
Accepted name: endogalactosaminidase
Reaction: Endohydrolysis of (1→4)-α-D-galactosaminidic linkages in poly(D-galactosamine)
Systematic name: galactosaminoglycan glycanohydrolase
References: [2091, 2509]

EC 3.2.1.109
[3.2.1.110 Deleted entry. mucinaminylserine mucaminidase. The enzyme is identical to EC 3.2.1.97, glycopeptide α-N-acetylgalactosaminidase]

EC 3.2.1.111
Accepted name: 1,3-α-L-fucosidase
Reaction: Hydrolysis of (1→3)-linkages between α-L-fucose and N-acetylglucosamine residues in glycoproteins
Other name(s): almond emulsin fucosidase I
Systematic name: 3-α-L-fucosyl-N-acetylgalcosaminyl-glycoprotein fucohydrolase
Comments: Not identical with EC 3.2.1.63 1,2-α-L-fucosidase.
References: [1084, 1863, 2895]

EC 3.2.1.112
Accepted name: 2-deoxyglucosidase
Reaction: a 2-deoxy-α-D-glucoside + H₂O = 2-deoxy-D-glucose + an alcohol
Other name(s): 2-deoxy-α-D-glucosidase; 2-deoxy-α-D-glucosidase
Systematic name: 2-deoxy-α-D-glucoside deoxyglucohydrolase
References: [335]

EC 3.2.1.113
Accepted name: mannosyl-oligosaccharide 1,2-α-mannosidase
Reaction: Hydrolysis of the terminal (1→2)-linked α-D-mannose residues in the oligo-mannose oligosaccharide Man₉(GlcNAc)₂
Other name(s): mannosidase 1A; mannosidase 1B; 1,2-α-mannosidase; exo-α-1,2-mannanase; mannose-9 processing α-mannosidase; glycoprotein processing mannosidase I; mannosidase I; Man₉-mannosidase; ManI; 1,2-α-mannosyl-oligosaccharide α-D-mannohydrolase
Systematic name: 2-α-mannosyl-oligosaccharide α-D-mannohydrolase
Comments: Involved in the synthesis of glycoproteins.
References: [2473, 2622]

EC 3.2.1.114
Accepted name: mannosyl-oligosaccharide 1,3-1,6-α-mannosidase
Reaction: Hydrolysis of the terminal (1→3)- and (1→6)-linked α-D-mannose residues in the mannosyl-oligosaccharide Man₅(GlcNAc)₃
Other name(s): mannosidase II; exo-1,3-1,6-α-mannosidase; α-D-mannosidase II; α-mannosidase II; α1-3,6-mannosidase; GlcNAc transferase I-dependent α1,3[α1,6]mannosidase; Golgi α-mannosidase II; ManII; 1,3(1,6)-α-D-mannosidase; 1,3-(1,6)-mannosyl-oligosaccharide α-D-mannohydrolase

Systematic name: (1→3)-(1→6)-mannosyl-oligosaccharide α-D-mannohydrolase

Comments: Involved in the synthesis of glycoproteins.

References: [931, 2622, 2623, 78]

[EC 3.2.1.114 created 1986]

EC 3.2.1.115

Accepted name: branched-dextran exo-1,2-α-glucosidase

Reaction: Hydrolysis of (1→2)-α-D-glucosidic linkages at the branch points of dextrans and related polysaccharides, producing free D-glucose

Other name(s): dextran 1,2-α-glucosidase; dextran α-1,2 debranching enzyme 1,2-α-D-glucosyl-branched-dextran 2-glucohydrolase

Systematic name: (1→2)-α-D-glucosyl-branched-dextran 2-glucohydrolase

Comments: Does not hydrolyse disaccharides or oligosaccharides containing linear 1,2-α-glucosidic linkages.

References: [1676, 1677]

[EC 3.2.1.115 created 1989]

EC 3.2.1.116

Accepted name: glucan 1,4-α-maltotriohydrolase

Reaction: Hydrolysis of (1→4)-α-D-glucosidic linkages in amylaceous polysaccharides, to remove successive maltotriose residues from the non-reducing chain ends

Other name(s): exo-maltotriohydrolase; maltotriohydrolase; 1,4-α-D-glucan maltotriohydrolase

Systematic name: 4-α-D-glucan maltotriohydrolase

Comments: Cf. EC 3.2.1.2 (β-amylase), EC 3.2.1.60 (glucan 1,4-α-maltotetraohydrolase) and EC 3.2.1.98 (glucan 1,4-α-maltohexaosidase). The products have the α-configuration.

References: [1773]

[EC 3.2.1.116 created 1989]

EC 3.2.1.117

Accepted name: amygndalin β-glucosidase

Reaction: (R)-amygdalin + H₂O = (R)-prunasin + D-glucose

Other name(s): amygdalase; amygdalinase; amygdalin hydrolase; amygdalin glucosidase

Systematic name: amygdalin β-D-glucohydrolase

Comments: Highly specific; does not act on prunasin, linamarin, gentiobiose or cellobiose (cf. EC 3.2.1.21 β-glucosidase).

References: [1362]

[EC 3.2.1.117 created 1989]

EC 3.2.1.118

Accepted name: prunasin β-glucosidase

Reaction: (R)-prunasin + H₂O = D-glucose + mandelonitrile

Other name(s): prunasin hydrolase

Systematic name: prunasin β-D-glucohydrolase

Comments: Highly specific; does not act on amygdalin, linamarin or gentiobiose. (cf. EC 3.2.1.21 β-glucosidase).

References: [1362]

[EC 3.2.1.118 created 1989]
EC 3.2.1.119
Accepted name: vicianin β-glucosidase
Reaction: \((R)-\text{vicianin} + \text{H}_2\text{O} = \text{mandelonitrile} + \text{vicianose}\)
Other name(s): vicianin hydrolase
Systematic name: \((R)-\text{vicianin} \beta-\text{D-glucohydrolase}\)
Comments: Also hydrolyses, more slowly, \((R)-\text{amygdalin}\) and \((R)-\text{prunasin}\), but not gentiobiose, linamarin or cellobiose.
References: [1362]

[EC 3.2.1.119 created 1989]

EC 3.2.1.120
Accepted name: oligoxyloglucan β-glycosidase
Reaction: Hydrolysis of \((1\rightarrow4)\)-β-D-glucosidic links in oligoxyloglucans so as to remove successive isoprimeverose [i.e. α-\text{xylo-}(1\rightarrow6)-β-D-glucosyl-] residues from the non-reducing chain ends
Other name(s): isoprimeverose-producing oligoxyloglucan hydrolase; oligoxyloglucan hydrolase
Systematic name: oligoxyloglucan xyloglucohydrolase
References: [1216]

[EC 3.2.1.120 created 1989]

EC 3.2.1.121
Accepted name: polymannuronate hydrolase
Reaction: Endohydrolysis of the D-mannuronide linkages of polymannuronate
Other name(s): polymannuronic acid polymerase
Systematic name: poly(mannuronide) mannuronohydrolase
Comments: Does not act on alginic acid, which is a copolymer of polymannuronate.
References: [597]

[EC 3.2.1.121 created 1989]

EC 3.2.1.122
Accepted name: maltose-6′-phosphate glucosidase
Reaction: maltose 6′-phosphate + \text{H}_2\text{O} = \text{D-glucose} + \text{D-glucose 6-phosphate}
Other name(s): phosho-α-glucosidase
Systematic name: maltose-6′-phosphate 6-phosphoglucohydrolase
Comments: Hydrolyses a variety of 6-phospho-D-glucosides, including maltose 6-phosphate, α,α-trehalose 6-phosphate, sucrose 6-phosphate and \(\beta\)-nitrophenyl-α-D-glucopyranoside 6-phosphate (as a chromogenic substrate). The enzyme is activated by Fe\text{II}, Mn\text{II}, Co\text{II} and Ni\text{II}. It is rapidly inactivated in air.
References: [2555]

[EC 3.2.1.122 created 1989, modified 1999]

EC 3.2.1.123
Accepted name: endoglycosylceramidase
Reaction: oligoglycosylglucosyl-(1→1)-ceramide + \text{H}_2\text{O} = \text{ceramide} + \text{oligoglycosylglucose}
Other name(s): endoglycoceramidase; EGCase; glycosyl-N-acetylsphingosine 1,1-β-D-glucanohydrolase, oligoglycosylglucosylceramide glycohydrolase; oligoglycosylglucosyl(1→1)ceramide glycohydrolase
Systematic name: oligoglycosylglucosyl-(1→1)-ceramide glycohydrolase
Comments: An enzyme from \textit{Rhodococcus} sp. that degrades various acidic and neutral glycosphingolipids to oligosaccharides and ceramides, by cleaving a glucosyl bond. Does not act on monoglycosylceramides. \textit{cf}. EC 3.2.1.62 glycosylceramidase.
References: [1102]
EC 3.2.1.124

Accepted name: 3-deoxy-2-octulosonidase
Reaction: Endohydrolysis of the β-ketopyranosidic linkages of 3-deoxy-D-manno-2-octulosonate in capsular polysaccharides
Other name(s): 2-keto-3-deoxyoctonate hydrolase; octulosylono hydrolase; octulosyluransylono hydrolase
Systematic name: capsular-polysaccharide 3-deoxy-D-manno-2-octulosonohydrolase
Comments: The enzyme from a bacteriophage catalyses the depolymerization of capsular polysaccharides containing 3-deoxy-2-octulosonide in the cell wall of *Escherichia coli.*
References: [40]

EC 3.2.1.125

Accepted name: raucaffricine β-glucosidase
Reaction: raucaffricine + H₂O = D-glucose + vomilenine
Other name(s): raucaffricine β-D-glucosidase; raucaffricine glucosidase
Systematic name: raucaffricine β-D-glucohydrolase
Comments: Highly specific; some other ajmalan glucoside alkaloids are hydrolysed, but more slowly.
References: [2259]

EC 3.2.1.126

Accepted name: coniferin β-glucosidase
Reaction: coniferin + H₂O = D-glucose + coniferol
Other name(s): coniferin-hydrolyzing β-glucosidase
Systematic name: coniferin β-D-glucosidase
Comments: Also hydrolyses syringin, 4-cinnamyl alcohol β-glucoside and, more slowly, some other aryl β-glycosides. A plant cell-wall enzyme involved in the biosynthesis of lignin.
References: [1044, 1561]

EC 3.2.1.127

Accepted name: 1,6-α-L-fucosidase
Reaction: Hydrolysis of (1→6)-linkages between α-L-fucose and N-acetyl-D-glucosamine in glycopeptides such as immunoglobulin G glycopeptide and fucosyl-asialo-agalacto-fetuin
Other name(s): α-L-fucosidase; 1,6-L-fucosyl-N-acetyl-D-glucosaminylglycopeptide fucohydrolase
Systematic name: 6-L-fucosyl-N-acetyl-D-glucosaminylglycopeptide fucohydrolase
Comments: The enzyme from *Aspergillus niger* does not act on 1,2-, 1,3-, or 1,4-L-fucosyl linkages.
References: [2877]

EC 3.2.1.128

Accepted name: glycyrrhizinate β-glucuronidase
Reaction: glycyrrhizinate + H₂O = (1→2)-β-D-glucuronosyl-D-glucuronate + glycyrrhetinate
Other name(s): glycyrrhizin β-hydrolase; glycyrrhizin hydrolase; glycyrrhizinic acid hydrolase
Systematic name: glycyrrhizinate glucuronosylhydrolase
Comments: The enzyme from *Aspergillus niger* is specific for the hydrolysis of the triterpenoid glycoside glycyrrhizinate from roots of *Glycyrrhiza* sp.

References: [1738]

[EC 3.2.1.128 created 1989]

**EC 3.2.1.129**

Accepted name: endo-α-sialidase

Reaction: Endohydrolysis of (2→8)-α-sialosyl linkages in oligo- or poly(sialic) acids

Other name(s): endo-N-acetyleneuraminidase; endoneuraminidase; endo-N-acetylneuraminidase; poly(α-2,8-sialosyl)
endo-N-acetylneuraminidase; poly(α-2,8-sialoside) α-2,8-sialosylhydrolase; endosialidase; endo-N polysialoside (2→8)-α-sialosylhydrolase

Comments: Although the name endo-N-acetylneuraminidase has also been used for this enzyme, this is misleading since its activity is not restricted to acetylated substrates. An exo-α-sialidase activity is listed as EC 3.2.1.18 exo-α-sialidase. See also EC 4.2.2.15 anhydroisialidase.

References: [687, 910, 1277, 1367, 1956, 2572, 318]

[EC 3.2.1.129 created 1990, modified 1999]

**EC 3.2.1.130**

Accepted name: glycoprotein endo-α-1,2-mannosidase

Reaction: Hydrolysis of the terminal α-D-glucosyl-(1,3)-D-mannosyl unit from the GlcMan9(GlcNAc)2 oligosaccharide component of the glycoprotein produced in the Golgi membrane

Other name(s): glucosylmannosidase; endo-α-D-mannosidase; endo-α-mannosidase; endomannosidase; glucosyl mannosidase

Systematic name: glycoprotein glucosylmannohydrolase

Comments: Involved in the synthesis of glycoproteins.

References: [1506, 2621]

[EC 3.2.1.130 created 1990]

**EC 3.2.1.131**

Accepted name: xylan α-1,2-glucuronosidase

Reaction: Hydrolysis of (1→2)-α-D-(4-O-methyl)glucuronosyl links in the main chain of hardwood xylans

Other name(s): 1,2-α-glucuronidase; α-(1→2)-glucuronidase; xylan α-D-1,2-(4-O-methyl)glucuronohydrolase

Systematic name: xylan 2-α-D-(4-O-methyl)glucuronohydrolase

References: [1098]

[EC 3.2.1.131 created 1990]

**EC 3.2.1.132**

Accepted name: chitosanase

Reaction: Endohydrolysis of β-(1→4)-linkages between D-glucosamine residues in a partly acetylated chitosan

Systematic name: chitosan N-acetylgalactosaminohydrolase

Comments: A whole spectrum of chitosanases are now known (for more details, see http://pages.usherbrooke.ca/rbrzezinski/). They can hydrolyse various types of links in chitosan. The only constant property is the endohydrolysis of GlcN-GlcN links, which is common to all known chitosanases. One known chitosanase is limited to this link recognition [1562], while the majority can also recognize GlcN-GlcNAc links or GlcNAc-GlcN links but not both. They also do not recognize GlcNAc-GlcNAc links in partly acetylated chitosan.

References: [677, 2181, 1112, 1562]

[EC 3.2.1.132 created 1990, modified 2004]

103
EC 3.2.1.133

**Accepted name:** glucan 1,4-\(\alpha\)-maltohydrolase  
**Reaction:** hydrolysis of (1\(\rightarrow\)4)-\(\alpha\)-D-glucosidic linkages in polysaccharides so as to remove successive \(\alpha\)-maltose residues from the non-reducing ends of the chains  
**Other name(s):** maltogenic \(\alpha\)-amylase; 1,4-\(\alpha\)-D-glucan \(\alpha\)-maltohydrolase  
**Systematic name:** 4-\(\alpha\)-D-glucan \(\alpha\)-maltohydrolase  
**Comments:** Acts on starch and related polysaccharides and oligosaccharides. The product is \(\alpha\)-maltose; *cf.* EC 3.2.1.2 \(\beta\)-amylase.  
**References:** [539, 1923]

[EC 3.2.1.133 created 1992, modified 1999]

EC 3.2.1.134

**Accepted name:** difructose-anhydride synthase  
**Reaction:** bis-D-fructose 2\(\prime\),1:2,1\(\prime\)-dianhydride + H\(_2\)O = inulobiose  
**Other name(s):** inulobiose hydrolase  
**Systematic name:** bis-D-fructose 2\(\prime\),1:2,1\(\prime\)-dianhydride fructohydrolase  
**Comments:** Produces difructose anhydride by the reverse reaction of partial hydrolysis, forming an \(\alpha\)-fructosidic linkage.  
**References:** [1594, 1595]

[EC 3.2.1.134 created 1992]

EC 3.2.1.135

**Accepted name:** neopullulanase  
**Reaction:** Hydrolysis of pullulan to panose (6-\(\alpha\)-D-glucosylmaltose)  
**Other name(s):** pullulanase II  
**Systematic name:** pullulan 4-\(\alpha\)-glucanohydrolase (panose-forming)  
**Comments:** *cf.* EC 3.2.1.41 (pullulanase ) and EC 3.2.1.57 (isopullulanase).  
**References:** [1083]

[EC 3.2.1.135 created 1992]

EC 3.2.1.136

**Accepted name:** glucuronoarabinoxylan endo-1,4-\(\beta\)-xylanase  
**Reaction:** Endohydrolysis of (1\(\rightarrow\)4)-\(\beta\)-D-xylosyl links in some glucuronoarabinoxylans  
**Other name(s):** feraxan endoxylanase; feraxanase; endoarabinoxylanase; glucuronoxylan xylohydrolase; glucuronoxylanase; glucuronoarabinoxylan 1,4-\(\beta\)-D-xylanohydrolase  
**Systematic name:** glucuronoarabinoxylan 4-\(\beta\)-D-xylanohydrolase  
**Comments:** High activity towards feruloylated arabinoxylans from cereal plant cell walls.  
**References:** [1817]

[EC 3.2.1.136 created 1992]

EC 3.2.1.137

**Accepted name:** mannan exo-1,2-1,6-\(\alpha\)-mannosidase  
**Reaction:** Hydrolysis of (1\(\rightarrow\)2)-\(\alpha\)-D- and (1\(\rightarrow\)6)-\(\alpha\)-D- linkages in yeast mannan, releasing D-mannose  
**Other name(s):** exo-1,2-1,6-\(\alpha\)-mannosidase; 1,2,1,6-\(\alpha\)-D-mannan D-mannohydrolase  
**Systematic name:** (1\(\rightarrow\)2)-(1\(\rightarrow\)6)-\(\alpha\)-D-mannan D-mannohydrolase  
**Comments:** Mannose residues linked \(\alpha\)-D-1,3- are also released, but very slowly.  
**References:** [2500]

[EC 3.2.1.137 created 1992]
EC 3.2.1.138  Transferred entry. anhydrosialidase. Now EC 4.2.2.15, anhydrosialidase

[EC 3.2.1.138 created 1992, deleted 2003]

EC 3.2.1.139

Accepted name: α-glucuronidase

Reaction: an α-D-glucuronoside + H₂O = an alcohol + D-glucuronate

Other name(s): α-glucosidurone

Systematic name: α-D-glucosiduronate glucuronohydrolase

Comments: Considerable differences in the specificities of the enzymes from different fungi for α-D-glucosiduronates have been reported. Activity is also found in the snail.

References: [2022, 2634]

[EC 3.2.1.139 created 1999]

EC 3.2.1.140

Accepted name: lacto-N-biosidase

Reaction: (1) β-D-Gal-(1→3)-β-D GlcNAc-(1→3)-β-D-Gal-(1→4)-D-Glc + H₂O = β-D-Gal-(1→3)-D-GlcNAc + β-D-Gal-(1→4)-D-Glc

(2) lacto-N-tetraose + H₂O = lacto-N-biose + lactose

Systematic name: oligosaccharide lacto-N-biosylhydrolase

Comments: The enzyme from Streptomyces specifically hydrolysates the terminal lacto-N-biosyl residue (β-D-Gal-(1→3)-D-GlcNAc) from the non-reducing end of oligosaccharides with the structure β-D-Gal-(1→3)-β-D-GlcNAc-(1→3)-β-D-Gal-(1→4)-β-D-GlcNAc-(1→4)-β-D-Gal-(1→4)-D-Glc to form first lacto-N-tetraose plus lacto-N-biose, with the subsequent formation of lactose. Oligosaccharides in which the non-reducing terminal Gal or the penultimate GlcNAc are replaced by fucose or sialic acid are not substrates. Asialo GM1 tetraose (β-D-Gal-(1→3)-β-D-GalNAc-(1→3)-β-D-Gal-(1→4)-D-Glc) is hydrolysed very slowly, but lacto-N-neotetraose (β-D-Gal-(1→4)-β-D-GalNAc-(1→3)-β-D-Gal-(1→4)-D-Glc) is not a substrate.

References: [2200, 2201]

[EC 3.2.1.140 created 1999]

EC 3.2.1.141

Accepted name: 4-α-D-(1→4)-α-D-glucanotrehalose trehalohydrolase

Reaction: hydrolysis of (1→4)-α-D-glucosidic linkage in 4-α-D-[(1→4)-α-D-glucanosyl]n trehalose to yield trehalose and (1→4)-α-D-glucan

Other name(s): malto-oligosyltrehalose trehalohydrolase

Systematic name: 4-α-D-[(1→4)-α-D-glucano]trehalose glucanohydrolase (trehalose-producing)

References: [1580, 1761, 1760]

[EC 3.2.1.141 created 1999]

EC 3.2.1.142

Accepted name: limit dextrinase

Reaction: Hydrolysis of (1→6)-α-D-glucosidic linkages in α- and β-limit dextrans of amylopectin and glycogen, and in amylopectin and pullulan

Other name(s): R-enzyme; amylopectin-1,6-glucosidase; dextrin α-1,6-glucanohydrolase

Systematic name: dextrin 6-α-glucanohydrolase

Comments: Plant enzymes with little or no action on glycogen. Action on amylopectin is incomplete, but action on α-limit dextrans is complete. Maltose is the smallest sugar it can release from an α-(1→6)-linkage.

References: [851, 1556]
EC 3.2.1.143
Accepted name: poly(ADP-ribose) glycohydrolase
Reaction: hydrolyses poly(ADP-ribose) at glycosidic (1''-2') linkage of ribose-ribose bond to produce free ADP-ribose
Comments: Specific to (1''-2') linkage of ribose-ribose bond of poly(ADP-ribose).
References: [1678, 1465]

EC 3.2.1.144
Accepted name: 3-deoxyoctulosonase
Reaction: 3-deoxyoctulosonyl-lipopolysaccharide + H₂O = 3-deoxyoctulosonic acid + lipopolysaccharide
Other name(s): α-Kdo-ase
Systematic name: 3-deoxyoctulosonyl-lipopolysaccharide hydrolase
Comments: Releases Kdo (α- and β-linked 3-deoxy-D-manno-octulosonic acid) from different lipopolysaccharides, including Re-LPS from Escherichia coli and Salmonella, Rd-LPS from S. minnesota, and de-O-acyl-re-LPS. 4-Methylumbelliferyl-α-Kdo (α-Kdo-OMec) is also a substrate.
References: [1448]

EC 3.2.1.145
Accepted name: galactan 1,3-β-galactosidase
Reaction: Hydrolysis of terminal, non-reducing β-D-galactose residues in (1→3)-β-D-galactopyranans
Other name(s): galactan (1→3)-β-D-galactosidase
Systematic name: galactan 3-β-D-galactosidase
Comments: This enzyme removes not only free galactose, but also 6-glycosylated residues, e.g., (1→6)-β-D-galactobiose, and galactose bearing oligosaccharide chains on O-6. Hence, it releases branches from [arabinono-galacto-(1→6)](1→3)-β-D-galactans.
References: [2611, 1957]

EC 3.2.1.146
Accepted name: β-galactofuranosidase
Reaction: Hydrolysis of terminal non-reducing β-D-galactofuranosides, releasing galactose
Other name(s): exo-β-galactofuranosidase; exo-β-D-galactofuranosidase; β-D-galactofuranosidase
Systematic name: β-D-galactofuranoside hydrolase
Comments: The enzyme from Helminthosporium sacchari detoxifies helminthosporoside, a bis(digalactosyl)terpene produced by this fungus, by releasing its four molecules of bound galactose.
References: [2111, 472, 447, 1657]

EC 3.2.1.147
Accepted name: thioglucosidase
Reaction: a thioglucoside + H₂O = a sugar + a thiol
Other name(s): myrosinase; sinigrinase; sinigrase
Systematic name: thioglucoside glucohydrolase
Comments: Has a wide specificity for thioglycosides.
References: [849, 1980]
EC 3.2.1.149

**Accepted name:** β-primeverosidase  
**Reaction:** a 6-O-(β-D-xlyopyranosyl)-β-D-glucopyranoside + H₂O = 6-O-(β-D-xlyopyranosyl)-β-D-glucopyranose + an alcohol  
**Systematic name:** 6-O-(β-D-xlyopyranosyl)-β-D-glucopyranoside 6-O-(β-D-xylosyl)-β-D-glucohydrolase  
**Comments:** The enzyme is responsible for the formation of the alcoholic aroma in oolong and black tea. In addition to β-primeverosides [i.e. 6-O-(β-D-xlyopyranosyl)-β-D-glucopyranoside], it also hydrolyses 6-O-(β-D-apiofuranosyl)-β-D-glucopyranosides and, less rapidly, β-vicianosides and 6-O-(α-L-arabinofuranosyl)-β-D-glucopyranosides, but not β-glucosides. Geranyl-, linaloyl-, benzyl- and p-nitrophenoxy glycosides are all hydrolysed.

**References:** [1074, 1868]

[EC 3.2.1.149 created 2001]

EC 3.2.1.150

**Accepted name:** oligoxyloglucan reducing-end-specific celllobiohydrolase  
**Reaction:** Hydrolysis of cellbiose from the reducing end of xyloglucans consisting of a (1→4)-β-linked glucan carrying α-D-xylosyl groups on O-6 of the glucose residues. To be a substrate, the first residue must be unsubstituted, the second residue may bear a xylosyl group, whether further glycosylated or not, and the third residue, which becomes the new terminus by the action of the enzyme, is preferably xylosylated, but this xylose residue must not be further substituted.  
**Systematic name:** oligoxyloglucan reducing-end celllobiohydrolase  
**Comments:** The enzyme is found in the fungus Geotrichum sp. M128. The substrate is a hemicellulose found in plant cell walls.

**References:** [2864]

[EC 3.2.1.150 created 2003]

EC 3.2.1.151

**Accepted name:** xyloglucan-specific endo-β-1,4-glucanase  
**Reaction:** xyloglucan + H₂O = xyloglucan oligosaccharides  
**Other name(s):** XEG; xyloglucan endo-β-1,4-glucanase; xyloglucanase; xyloglucanendohydrolase; XH; 1,4-β-D-glucan glucohydrolase  
**Systematic name:** [(1→6)-α-D-xylo]-[(1→4)-β-D-glucan glucohydrolase  
**Comments:** The enzyme from Aspergillus aculeatus is specific for xyloglucan and does not hydrolyse other cell-wall components. The reaction involves endohydrolysis of 1,4-β-D-glucosidic linkages in xyloglucan with retention of the β-configuration of the glycosyl residues.

**References:** [1949, 875]

[EC 3.2.1.151 created 2003]

EC 3.2.1.152

**Accepted name:** mannosylglycoprotein endo-β-mannosidase  
**Reaction:** Hydrolysis of the α-D-mannosyl-(1→6)-β-D-mannosyl-(1→4)-β-D-N-acetylglucosaminyl-(1→4)-β-D-N-acetylglucosaminyl sequence of glycoprotein to α-D-mannosyl-(1→6)-D-mannose and β-D-N-acetylglucosaminyl-(1→4)-β-D-N-acetylglucosaminyl sequences

**Other name(s):** endo-β-mannosidase
**Comments:** The substrate group is a substituent on N-4 of an asparagine residue in the glycoprotein. The mannose residue at the non-reducing end of the sequence may carry further α-D-mannosyl groups on O-3 or O-6, but such a substituent on O-3 of the β-D-mannosyl group prevents the action of the enzyme. The enzyme was obtained from the lily, *Lilium longiflorum.*

**References:** [1100, 2211]

[EC 3.2.1.152 created 2005]

**EC 3.2.1.153**

**Accepted name:** fructan β-(2,1)-fructosidase  
**Reaction:** Hydrolysis of terminal, non-reducing (2→1)-linked β-D-fructofuranose residues in fructans  
**Other name(s):** β-(2,1)-fructan fructohydrolase; β-(2,1)-fructan exohydrolase; inulinase; 1-FEH II; 1-fructan exohydrolase; 1-FEH w1; 1-FEH w2; β-(2,1)-linkage-specific fructan-β-fructosidase; β-(2,1)-D-fructan fructohydrolase  
**Systematic name:** β-(2→1)-D-fructan fructohydrolase  
**Comments:** Possesses one of the activities of EC 3.2.1.80, fructan β-fructosidase. While the best substrates are the inulin-type fructans, such as 1-kestose [β-D-fructofuranosyl-(2→1)-β-D-fructofuranosyl α-D-glucopyranoside] and 1,1-nystose [β-D-fructofuranosyl-(2→1)-β-D-fructofuranosyl-(2→1)-β-D-fructofuranosyl α-D-glucopyranoside], some (but not all) levan-type fructans can also be hydrolysed, but more slowly [see EC 3.2.1.154, fructan β-(2,6)-fructosidase]. Sucrose, while being a very poor substrate, can substantially inhibit enzyme activity in some cases.

**References:** [2143, 518]

[EC 3.2.1.153 created 2005]

**EC 3.2.1.154**

**Accepted name:** fructan β-(2,6)-fructosidase  
**Reaction:** Hydrolysis of terminal, non-reducing (2→6)-linked β-D-fructofuranose residues in fructans  
**Other name(s):** β-(2,6)-fructan exohydrolase; levanase; 6-FEH; β-(2,6)-D-fructan fructohydrolase  
**Systematic name:** (2→6)-β-D-fructan fructohydrolase  
**Comments:** Possesses one of the activities of EC 3.2.1.80, fructan β-fructosidase. While the best substrates are the levan-type fructans such as 6-kestotriose [β-D-fructofuranosyl-(2→6)-β-D-fructofuranosyl α-D-glucopyranoside] and 6,6-kestotetraose [β-D-fructofuranosyl-(2→6)-β-D-fructofuranosyl-(2→6)-β-D-fructofuranosyl α-D-glucopyranoside], some (but not all) inulin-type fructans can also be hydrolysed, but more slowly [cf. EC 3.2.1.153, fructan β-(2,1)-fructosidase]. Sucrose, while being a very poor substrate, can substantially inhibit enzyme activity in some cases.

**References:** [1582, 519, 986]

[EC 3.2.1.154 created 2005]

**EC 3.2.1.155**

**Accepted name:** xyloglucan-specific exo-β-1,4-glucanase  
**Reaction:** xyloglucan + H₂O = xyloglucan oligosaccharides [exohydrolysis of (1→4)-β-D-glucosidic linkages in xyloglucan]  
**Other name(s):** Cel74A  
**Systematic name:** [(1→6)-α-D-xylol]-1→4)-β-D-glucan exo-glucohydrolase  
**Comments:** The enzyme from *Chrysosporium lucknowense* is an endoglucanase, i.e. acquires the specificity of EC 3.2.1.151, xyloglucan-specific endo-β-1,4-glucanase, when it acts on linear substrates without bulky substituents on the polymeric backbone (e.g. carboxymethylcellulose). However, it switches to an exoglucanase mode of action when bulky side chains are present (as in the case of xyloglucan). The enzyme can also act on barley β-glucan, but more slowly.

**References:** [875]

[EC 3.2.1.155 created 2005, withdrawn at public-review stage, modified and reinstated 2006]
<table>
<thead>
<tr>
<th>EC 3.2.1.156</th>
<th>oligosaccharide reducing-end xylanase</th>
<th>Hydrolysis of (1→4)-β-D-xylose residues from the reducing end of oligosaccharides</th>
</tr>
</thead>
<tbody>
<tr>
<td>Accepted name:</td>
<td>oligosaccharide reducing-end xylanase</td>
<td>Hydrolysis of (1→4)-β-D-xylose residues from the reducing end of oligosaccharides</td>
</tr>
<tr>
<td>Reaction:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other name(s):</td>
<td>Rex; reducing end xylose-releasing exo-oligoxylanase</td>
<td></td>
</tr>
<tr>
<td>Systematic name:</td>
<td>β-D-xylopyranosyl-(1→4)-β-D-xylopyranose reducing-end xylanase</td>
<td></td>
</tr>
<tr>
<td>Comments:</td>
<td>The enzyme acts rapidly on the β-anomer of β-D-xylopyranosyl-(1→4)-β-D-xylopyranose, leaving the new reducing end in the α configuration. It also acts on longer oligosaccharides that have this structure at their reducing ends. The penultimate residue must be xylose, but replacing either of the other two residues with glucose merely slows the rate greatly.</td>
<td></td>
</tr>
<tr>
<td>References:</td>
<td>[1031, 770]</td>
<td>[EC 3.2.1.156 created 2005]</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>EC 3.2.1.157</th>
<th>t-carrageenase</th>
<th>Endohydrolysis of (1→4)-β-D-linkages between D-galactose 4-sulfate and 3,6-anhydro-D-galactose-2-sulfate in t-carrageenans</th>
</tr>
</thead>
<tbody>
<tr>
<td>Accepted name:</td>
<td>t-carrageenase</td>
<td>Endohydrolysis of (1→4)-β-D-linkages between D-galactose 4-sulfate and 3,6-anhydro-D-galactose-2-sulfate in t-carrageenans</td>
</tr>
<tr>
<td>Reaction:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Systematic name:</td>
<td>t-carrageenan 4-β-D-glycanohydrolase (configuration-inverting)</td>
<td></td>
</tr>
<tr>
<td>Comments:</td>
<td>The main products of hydrolysis are t-neocarratetraose sulfate and t-neocarrahexaose sulfate. t-Neocarraoctaose is the shortest substrate oligomer that can be cleaved. Unlike EC 3.2.1.81, β-agarase and EC 3.2.1.83, κ-carrageenase, this enzyme proceeds with inversion of the anomeric configuration. t-Carrageenan differs from κ-carrageenan by possessing a sulfo group on O-2 of the 3,6-anhydro-D-galactose residues, in addition to that present in the κ-compound on O-4 of the D-galactose residues.</td>
<td></td>
</tr>
<tr>
<td>References:</td>
<td>[122, 1652, 1653]</td>
<td>[EC 3.2.1.157 created 2006]</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>EC 3.2.1.158</th>
<th>α-agarase</th>
<th>Endohydrolysis of (1→3)-α-L-galactosidic linkages in agarose, yielding agarotetraose as the major product</th>
</tr>
</thead>
<tbody>
<tr>
<td>Accepted name:</td>
<td>α-agarase</td>
<td>Endohydrolysis of (1→3)-α-L-galactosidic linkages in agarose, yielding agarotetraose as the major product</td>
</tr>
<tr>
<td>Reaction:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other name(s):</td>
<td>agarase (ambiguous); agaraseA33</td>
<td></td>
</tr>
<tr>
<td>Systematic name:</td>
<td>agarose 3-glycanohydrolase</td>
<td></td>
</tr>
<tr>
<td>Comments:</td>
<td>Requires Ca(^{2+}). The enzyme from Thalassomonas sp. can use agarose, agarohexaose and neoagarohexaose as substrate. The products of agarohexaose hydrolysis are dimers and tetramers, with agarotetraose being the predominant product, whereas hydrolysis of neoagarohexaose gives rise to two types of trimer. While the enzyme can also hydrolyse the highly sulfated agarose porphyran very efficiently, it cannot hydrolyse the related compounds κ-carrageenan (see EC 3.2.1.83) and t-carrageenan (see EC 3.2.1.157) [1882]. See also EC 3.2.1.81, β-agarase.</td>
<td></td>
</tr>
<tr>
<td>References:</td>
<td>[2012, 1882]</td>
<td>[EC 3.2.1.158 created 2006]</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>EC 3.2.1.159</th>
<th>α-neoagararo-oligosaccharide hydrolase</th>
<th>Hydrolysis of the (1→3)-α-L-galactosidic linkages of neoagararo-oligosaccharides that are smaller than a hexamer, yielding 3,6-anhydro-L-galactose and D-galactose</th>
</tr>
</thead>
<tbody>
<tr>
<td>Accepted name:</td>
<td>α-neoagararo-oligosaccharide hydrolase</td>
<td>Hydrolysis of the (1→3)-α-L-galactosidic linkages of neoagararo-oligosaccharides that are smaller than a hexamer, yielding 3,6-anhydro-L-galactose and D-galactose</td>
</tr>
<tr>
<td>Reaction:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other name(s):</td>
<td>α-neoagararo-oligosaccharide hydrolase; α-NAOS hydrolase</td>
<td></td>
</tr>
<tr>
<td>Systematic name:</td>
<td>α-neoagararo-oligosaccharide 3-glycohydrolase</td>
<td></td>
</tr>
<tr>
<td>Comments:</td>
<td>When neoagarohexaose is used as a substrate, the oligosaccharide is cleaved at the non-reducing end to produce 3,6-anhydro-L-galactose and agaropentaose, which is further hydrolysed to agarobiose and agarotriose. With neoagarotetraose as substrate, the products are predominantly agarotriose and 3,6-anhydro-L-galactose. In Vibrio sp. the actions of EC 3.2.1.81, β-agarase and EC 3.2.1.159 can be used to degrade agarose to 3,6-anhydro-L-galactose and D-galactose.</td>
<td></td>
</tr>
<tr>
<td>References:</td>
<td>[1882]</td>
<td>[EC 3.2.1.159 created 2006]</td>
</tr>
</tbody>
</table>
EC 3.2.1.161

Accepted name: β-apiosyl-β-glucosidase
Reaction: 7-[β-D-apiofuranosyl-(1→6)-β-D-glucopyranosyloxy]isoflavonoid + H₂O = a 7-hydroxyisoflavonoid + β-D-apiofuranosyl-(1→6)-D-glucose
Other name(s): isoflavonoid-7-O-β-[D-apiofuranosyl-(1→6)-β-D-glucoside] disaccharidase; isoflavonoid 7-O-glucoside β-glucosidase; furcatin hydrolase
Systematic name: 7-[β-D-apiofuranosyl-(1→6)-β-D-glucopyranosyloxy]isoflavonoid β-D-apiofuranosyl-(1→6)-D-glucohydrolase
Comments: The enzyme from the tropical tree Dalbergia nigrescens Kurz belongs in glycosyl hydrolase family 1. The enzyme removes disaccharides from the natural substrates dalpatein 7-O-glucoside and 7-hydroxy-2′,4′,5′,6-tetramethoxy-7-O-β-D-apiofuranosyl-(1→6)-β-D-glucopyranoside (dalnigrein 7-O-glucoside) although it can also remove a single glucose residue from isoflavonoid 7-O-glucosides [402]. Daidzin and genistin are also substrates.
References: [1043, 402, 23]

EC 3.2.1.162

Accepted name: λ-carrageenase
Reaction: Endohydrolysis of (1→4)-β-linkages in the backbone of λ-carrageenan, resulting in the tetrasaccharide α-D-Galp2,6,2′,6″-(1→3)-β-D-Galp2S-(1→4)-α-D-Galp2,6,2′,6″-(1→3)-D-Galp2S
Other name(s): endo-β-1,4-carrageenose 2,6,2′-trisulfate-hydrolase
Systematic name: endo-(1→4)-β-carrageenose 2,6,2′-trisulfate-hydrolase
Comments: The enzyme from Pseudoalteromonas sp. is specific for λ-carrageenan. 1-Carrageenan (see EC 3.2.1.157, 1-carrageenase), κ-carrageenan (see EC 3.2.1.83, κ-carrageenase), agarose and porphyran are not substrates.
References: [1881]

EC 3.2.1.163

Accepted name: 1,6-α-D-mannosidase
Reaction: Hydrolysis of the (1→6)-linked α-D-mannose residues in α-D-Manp-(1→6)-D-Manp
Systematic name: (1→6)-α-mannosyl α-D-mannohydrolase
Comments: The enzyme is specific for (1→6)-linked mannobiose and has no activity towards any other linkages, or towards p-nitrophenoxy-α-D-mannopyranoside or baker’s yeast mannan. It is strongly inhibited by Mn²⁺ but does not require Ca²⁺ or any other metal cofactor for activity.
References: [78]

EC 3.2.1.164

Accepted name: galactan endo-1,6-β-galactosidase
Reaction: Endohydrolysis of (1→6)-β-D-galactosidic linkages in arabinogalactan proteins and (1→3):(1→6)-β-galactans to yield galactose and (1→6)-β-galactobiose as the final products

Other name(s): endo-1,6-β-galactanase

Systematic name: endo-β-(1→6)-galactanase

Comments: The enzyme specifically hydrolyses 1,6-β-D-galactooligosaccharides with a degree of polymerization (DP) higher than 3, and their acidic derivatives with 4-O-methylglucosyluronate or glucosyluronate groups at the non-reducing terminals [1895]. 1,3-β-D- and 1,4-β-D-galactosyl residues cannot act as substrates. The enzyme can also hydrolyse α-L-arabinofuranosidase-treated arabinogalactan protein (AGP) extracted from radish roots [1895, 1317]. AGPs are thought to be involved in many physiological events, such as cell division, cell expansion and cell death [1317].

References: [270, 1895, 1317]

EC 3.2.1.165

Accepted name: exo-1,4-β-D-glucosaminidase

Reaction: Hydrolysis of chitosan or chitosan oligosaccharides to remove successive D-glucosamine residues from the non-reducing termini

Other name(s): CsxA; GlcNase; exochitosanase; GlmA; exo-β-D-glucosaminidase; chitosan exo-1,4-β-D-glucosaminidase

Systematic name: chitosan exo-(1→4)-β-D-glucosaminidase

Comments: Chitosan is a partially or totally N-deacetylated chitin derivative that is found in the cell walls of some phytopathogenic fungi and comprises D-glucosamine residues with a variable content of GlcNAc residues [445]. Acts specifically on chitooligosaccharides and chitosan, having maximal activity on chitotetraose, chitopentaose and their corresponding alcohols [1782]. The enzyme can degrade GlcN-GlcNAc but not GlcN-GlcNAc [758]. A member of the glycoside hydrolase family 2 (GH-2) [445].

References: [1782, 1822, 758, 445, 1075]

EC 3.2.2 Hydrolysing N-glycosyl compounds

EC 3.2.2.1

Accepted name: purine nucleosidase

Reaction: a purine nucleoside + H₂O = D-ribose + a purine base

Other name(s): nucleosidase; purine β-ribosidase; purine nucleoside hydrolase; purine ribonucleosidase; ribonucleoside hydrolase; nucleoside hydrolase; N-ribosyl purine ribohydrolase; nucleosidase g; N-D-ribosylpurine ribohydrolase; inosine-adenosine-guanosine preferring nucleoside hydrolase; purine-specific nucleoside N-ribohydrolase; IAG-nucleoside hydrolase; IAG-NH

Systematic name: purine-nucleoside ribohydrolase

Comments: The enzyme from the bacterium Ochrobactrum anthropi specifically catalyses the irreversible N-riboside hydrolysis of purine nucleosides. Pyrimidine nucleosides, purine and pyrimidine nucleotides, NAD⁺, NADP⁺ and nicotinamindine mononucleotide are not substrates [1867].

References: [989, 1179, 2480, 2531, 1941, 1867, 2692, 1609]

EC 3.2.2.2

Accepted name: inosine nucleosidase

Reaction: inosine + H₂O = D-ribose + hypoxanthine

Other name(s): inosinase; inosine-guanosine nucleosidase

Systematic name: inosine ribohydrolase

References: [1294, 2531]
EC 3.2.2.3
Accepted name: uridine nucleosidase
Reaction: uridine + H₂O → D-ribose + uracil
Other name(s): uridine hydrolase
Systematic name: uridine ribohydrolase
References: [343]

EC 3.2.2.4
Accepted name: AMP nucleosidase
Reaction: AMP + H₂O → D-ribose 5-phosphate + adenine
Other name(s): adenylate nucleosidase; adenosine monophosphate nucleosidase
Systematic name: AMP phosphoribohydrolase
References: [1063]

EC 3.2.2.5
Accepted name: NAD⁺ nucleosidase
Reaction: NAD⁺ + H₂O → ADP-ribose + nicotinamide
Other name(s): NADase; DPNase; DPN hydrolase; NAD hydrolase; diphosphopyridine nucleosidase; nicotinamide adenine dinucleotide nucleosidase; NAD glycohydrolase; NAD nucleosidase; nicotinamide adenine dinucleotide glycohydrolase
Systematic name: NAD⁺ glycohydrolase
Comments: This enzyme can also hydrolyse NADP⁺ to yield phospho-ADP-ribose and nicotinamide, but more slowly.
References: [1022, 1781, 2637, 2849]

EC 3.2.2.6
Accepted name: NAD(P)⁺ nucleosidase
Reaction: NAD(P)⁺ + H₂O → ADP-ribose(P) + nicotinamide
Other name(s): nicotinamide adenine dinucleotide (phosphate) nucleosidase; triphosphopyridine nucleotidase; NAD(P) nucleosidase; NAD(P)ase; nicotinamide adenine dinucleotide (phosphate) glycohydrolase
Systematic name: NAD(P)⁺ glycohydrolase
Comments: Also catalyses transfer of ADP-ribose(P) residues.
References: [33, 2906, 2907]

EC 3.2.2.7
Accepted name: adenosine nucleosidase
Reaction: adenosine + H₂O → D-ribose + adenine
Other name(s): adenosinase; N-ribosyladenine ribohydrolase; adenosine hydrolase; ANase
Systematic name: adenosine ribohydrolase
Comments: Also acts on adenosine N-oxide.
References: [1607]
**EC 3.2.2.8**

**Accepted name:** ribosylpyrimidine nucleosidase  
**Reaction:** a pyrimidine nucleoside + H₂O = D-ribose + a pyrimidine base  
**Other name(s):**  
- N-ribosylpyrimidine nucleosidase; pyrimidine nucleosidase; N-ribosylpyrimidine ribohydrolase;  
- pyrimidine nucleoside hydrolase; RihB; YeiK; nucleoside ribohydrolase  
**Systematic name:** pyrimidine-nucleoside ribohydrolase  
**Comments:** Also hydrolyses purine D-ribonucleosides, but much more slowly. 2', 3' and 5'-deoxynucleosides are not substrates [806].  
**References:** [2540, 1961, 806, 807]

[EC 3.2.2.8 created 1972]

**EC 3.2.2.9**

**Accepted name:** adenosylhomocysteine nucleosidase  
**Reaction:** S-adenosyl-L-homocysteine + H₂O = S-(5-deoxy-D-ribo-5-yl)-L-homocysteine + adenine  
**Other name(s):**  
- S-adenosylhomocysteine hydrolase (ambiguous); S-adenosylhomocysteine nucleosidase; 5'-methyladenosine nucleosidase; S-adenosylhomocysteine/5'-methylthioadenosine nucleosidase; Ado-Hcy/MTA nucleosidase  
**Systematic name:** S-adenosyl-L-homocysteine homocysteinylribohydrolase  
**Comments:** Also acts on S-methyl-5'-thioadenosine to give adenine and S-methyl-5-thioribose (cf. EC 3.2.2.16, methylthioadenosine nucleosidase).  
**References:** [591, 680]

[EC 3.2.2.9 created 1972, modified 2004]

**EC 3.2.2.10**

**Accepted name:** pyrimidine-5'-nucleotide nucleosidase  
**Reaction:** a pyrimidine 5'-nucleotide + H₂O = D-ribose 5-phosphate + a pyrimidine base  
**Other name(s):** pyrimidine nucleotide N-ribosidase; Pyr5N  
**Systematic name:** pyrimidine-5'-nucleotide phosphoribo(deoxyribo)hydrolase  
**Comments:** Also acts on dUMP, dTMP and dCMP.  
**References:** [1079, 1080]

[EC 3.2.2.10 created 1972]

**EC 3.2.2.11**

**Accepted name:** β-aspartyl-N-acetylglucosaminidase  
**Reaction:** 1-β-aspartyl-N-acetyl-D-glucosaminylamine + H₂O = L-asparagine + N-acetyl-D-glucosamine  
**Other name(s):** β-aspartylacetylglucosaminidase  
**Systematic name:** 1-β-aspartyl-N-acetyl-D-glucosaminylamine L-asparaginohydrolase  
**References:** [652]

[EC 3.2.2.11 created 1972]

**EC 3.2.2.12**

**Accepted name:** inosinate nucleosidase  
**Reaction:** 5'-inosinate + H₂O = D-ribose 5-phosphate + hypoxanthine  
**Systematic name:** 5'-inosinate phosphoribohydrolase  
**References:** [1346]

[EC 3.2.2.7 created 1972]
EC 3.2.2.12

Accepted name: 1-methyladenosine nucleosidase
Reaction: 1-methyladenosine + H$_2$O = 1-methyladenine + D-ribose
Other name(s): 1-methyladenosine hydrolase
Systematic name: 1-methyladenosine ribohydrolase
References: [2532]

EC 3.2.2.13

Accepted name: NMN nucleosidase
Reaction: nicotinamide D-ribonucleotide + H$_2$O = D-ribose 5-phosphate + nicotinamide
Other name(s): NMNase; nicotinamide mononucleotide nucleosidase; nicotinamide mononucleotidase; NMN glyco-
hydrolyase; NMNGhase
Systematic name: nicotinamide-nucleotide phosphoribohydrolase
References: [51]

EC 3.2.2.14

Accepted name: DNA-deoxyinosine glycosylase
Reaction: Hydrolyses DNA and polynucleotides, releasing free hypoxanthine
Other name(s): DNA(hypoxanthine) glycohydrolase; deoxyribonucleic acid glycosylase; hypoxanthine-DNA glyco-
sylase
Systematic name: DNA-deoxyinosine deoxyribohydrolase
References: [1204]

EC 3.2.2.15

Accepted name: methylthioadenosine nucleosidase
Reaction: S-methyl-5′-thioadenosine + H$_2$O = S-methyl-5-thio-D-ribose + adenine
Other name(s): 5′-methylthioadenosine nucleosidase; MTA nucleosidase; MeSAdo nucleosidase; methylthioadeno-
sine methylthioribohydrolase
Systematic name: S-methyl-5′-thioadenosine adeninehydrolase
Comments: Does not act on S-adenosylhomocysteine. cf. EC 3.2.2.9 adenosylhomocysteine nucleosidase.
References: [892]

EC 3.2.2.16

Accepted name: deoxyribodipyrimidine endonucleosidase
Reaction: Cleaves the N-glycosidic bond between the 5′-pyrimidine residue in cyclobutadipyrimidine (in DNA) and the corresponding deoxy-D-ribose residue
Other name(s): pyrimidine dimer DNA-glycosylase; endonuclease V; deoxyribonucleate pyrimidine dimer glycosi-
dase; pyrimidine dimer DNA glycosylase; T$_4$-induced UV endonuclease; PD-DNA glycosylase
Systematic name: deoxy-D-ribo cyclobutadipyrimidine polynucleotidodeoxyribohydrolase
References: [943]
Deleted entry. Glycopeptide N-glycosidase. Now included with EC 3.5.1.52, peptide-N\textsuperscript{4}-(N-acetyl-\textbeta-glucosaminyl)asparagine amidase.

[EC 3.2.2.18 created 1984, deleted 1989]

EC 3.2.2.19

**Accepted name:** [protein ADP-ribosylarginine] hydrolase

**Reaction:**

(1) protein-\textit{N}\textsuperscript{\omega}-(ADP-D-ribosyl)-L-arginine + H\textsubscript{2}O = ADP-ribose + protein-L-arginine

(2) \textit{N}\textsuperscript{\omega}-(ADP-D-ribosyl)-L-arginine + H\textsubscript{2}O = ADP-ribose + L-arginine

**Other name(s):** ADP-ribose-L-arginine cleavage enzyme; ADP-ribosylarginine hydrolase; \textit{N}\textsuperscript{\omega}-(ADP-D-ribosyl)-L-arginine ADP-ribosylhydrolase; protein-\textit{ω}-N-(ADP-D-ribosyl)-L-arginine ADP-ribosylhydrolase

**Systematic name:** protein-\textit{N}\textsuperscript{\omega}-(ADP-D-ribosyl)-L-arginine ADP-ribosylhydrolase

**Comments:** The enzyme will remove ADP-ribose from arginine residues in ADP-ribosylated proteins.

**References:** [1719, 1720, 1306, 2478, 1879]

[EC 3.2.2.19 created 1989, modified 2004]

EC 3.2.2.20

**Accepted name:** DNA-3-methyladenine glycosylase I

**Reaction:** Hydrolysis of alkylated DNA, releasing 3-methyladenine

**Other name(s):** deoxyribonucleate 3-methyladenine glycosidase I; 3-methyladenine DNA glycosylase I; DNA-3-methyladenine glycosidase I

**Systematic name:** alkylated-DNA glycohydrolase (releasing methyladenine and methylguanine)

**Comments:** Involved in the removal of alkylated bases from DNA in \textit{Escherichia coli} (cf. EC 2.1.1.63 methylated-DNA—[protein]-cysteine S-methyltransferase).

**References:** [649, 1203, 2553]

[EC 3.2.2.20 created 1990, modified 2000]

EC 3.2.2.21

**Accepted name:** DNA-3-methyladenine glycosylase II

**Reaction:** Hydrolysis of alkylated DNA, releasing 3-methyladenine, 3-methylguanine, 7-methylguanine and 7-methyladenine

**Other name(s):** deoxyribonucleate 3-methyladenine glycosidase II; 3-methyladenine DNA glycosylase II; DNA-3-methyladenine glycosidase II; AlkA

**Systematic name:** alkylated-DNA glycohydrolase (releasing methyladenine and methylguanine)

**Comments:** Involved in the removal of alkylated bases from DNA in \textit{Escherichia coli} (cf. EC 2.1.1.63 methylated-DNA—[protein]-cysteine S-methyltransferase).

**References:** [649, 1203, 2105, 2553]

[EC 3.2.2.21 created 1990, modified 2000]

EC 3.2.2.22

**Accepted name:** rRNA \textit{N}-glycosylase

**Reaction:** Hydrolysis of the \textit{N}-glycosylic bond at A-4324 in 28S rRNA from rat ribosomes

**Other name(s):** ribosomal ribonucleate \textit{N}-glycosidase; nigrin b; RNA \textit{N}-glycosidase; rRNA \textit{N}-glycosidase; ricin; momorcochin-S; Mirabilis antiviral protein; momorcochin-S; gelonin; saporins

**Systematic name:** rRNA \textit{N}-glycohydrolase

**Comments:** Ricin A-chain and related toxins show this activity. Naked rRNA is attacked more slowly than rRNA in intact ribosomes. Naked rRNA from \textit{Escherichia coli} is cleaved at a corresponding position.

**References:** [630]

[EC 3.2.2.22 created 1990, modified 2000]
EC 3.2.2.23

Accepted name: DNA-formamidopyrimidine glycosylase
Reaction: Hydrolysis of DNA containing ring-opened 7-methylguanine residues, releasing 2,6-diamino-4-hydroxy-5-(N-methyl)formamidopyrimidine
Other name(s): Fapy-DNA glycosylase; deoxyribonucleate glycosidase; 2,6-diamino-4-hydroxy-5N-formamidopyrimidine-DNA glycosylase; 2,6-diamino-4-hydroxy-5(N-methyl)formamidopyrimidine-DNA glycosylase; formamidopyrimidine-DNA glycosylase; DNA-formamidopyrimidine glycosidase; Fpg protein
Systematic name: DNA glycohydrolase [2,6-diamino-4-hydroxy-5-(N-methyl)formamidopyrimidine releasing]
Comments: May play a significant role in processes leading to recovery from mutagenesis and/or cell death by alkylating agents. Also involved in the GO system responsible for removing an oxidatively damaged form of guanine (7,8-dihydro-8-oxoguanine) from DNA.
References: [232]

[EC 3.2.2.23 created 1990, modified 2000]

EC 3.2.2.24

Accepted name: ADP-ribosyl-[dinitrogen reductase] hydrolase
Reaction: ADP-D-ribo-syl-[dinitrogen reductase] = ADP-D-ribose + [dinitrogen reductase]
Other name(s): azoferredoxin glycosidase; azoferredoxin-activating enzymes; dinitrogenase reductase-activating glycohydrolase; ADP-ribo-syl glycohydrolase
Systematic name: ADP-D-ribosyl-[dinitrogen reductase] ADP-ribosylhydrolase
Comments: Together with EC 2.4.2.37 NAD$^+$—dinitrogen-reductase ADP-D-ribo-syltransferase, this enzyme controls the level of activity of EC 1.18.6.1 nitrogenase.
References: [697]

[EC 3.2.2.24 created 1992]

EC 3.2.2.25

Accepted name: N-methyl nucleosidase
Reaction: 7-methylxanthosine + H$_2$O = 7-methylxanthine + D-ribose
Other name(s): 7-methylxanthosine nucleosidase; N-MeNase; N-methyl nucleoside hydrolase; methylpurine nucleosidase
Systematic name: 7-methylxanthosine ribohydrolase
Comments: The enzyme preferentially hydrolyses 3- and 7-methylpurine nucleosides, such as 3-methylxanthosine, 3-methyladenosine and 7-methylguanosine. Hydrolysis of 7-methylxanthosine to form 7-methylxanthine is the second step in the caffeine-biosynthesis pathway.
References: [1793]

[EC 3.2.2.25 created 2007]

EC 3.2.2.26

Accepted name: futalosine hydrolase
Reaction: futalosine + H$_2$O = dehypoxanthine futalosine + hypoxanthine
Other name(s): futalosine nucleosidase; MqnB
Systematic name: futalosine ribohydrolase
Comments: This enzyme, which is specific for futalosine, catalyses the second step of a novel menaquinone biosynthetic pathway that is found in some prokaryotes.
References: [1013]

[EC 3.2.2.26 created 2008]
Accepted name: uracil-DNA glycosylase
Reaction: Hydrolyses single-stranded DNA or mismatched double-stranded DNA and polynucleotides, releasing free uracil
Other name(s): UdgB (ambiguous); uracil-DNA N-glycosylase; UDG (ambiguous); uracil DNA glycohydrolase
Systematic name: uracil-DNA deoxyribohydrolase (uracil-releasing)
Comments: Uracil-DNA glycosylases are widespread enzymes that are found in all living organisms. EC 3.2.2.27 and double-stranded uracil-DNA glycosylase (EC 3.2.2.28) form a central part of the DNA-repair machinery since they initiate the DNA base-excision repair pathway by hydrolysing the N-glycosidic bond between uracil and the deoxyribose sugar thereby catalysing the removal of mis-incorporated uracil from DNA.
References: [1402, 1258, 1938, 2429]

[EC 3.2.2.27 created 2009]

EC 3.2.2.28
Accepted name: double-stranded uracil-DNA glycosylase
Reaction: Specifically hydrolyses mismatched double-stranded DNA and polynucleotides, releasing free uracil
Other name(s): Mug; double-strand uracil-DNA glycosylase; Dug; dsUDG; double-stranded DNA specific UDG; dsDNA specific UDG; UdgB (ambiguous); G:T/U mismatch-specific DNA glycosylase; UDG (ambiguous)
Systematic name: uracil-double-stranded DNA deoxyribohydrolase (uracil-releasing)
Comments: No activity on DNA containing a T/G mispair or single-stranded DNA containing either a site-specific uracil or 3,N4-ethenocytosine residue [2453], significant role for double-stranded uracil-DNA glycosylase in mutation avoidance in non-dividing E. coli [1690]. Uracil-DNA glycosylases are widespread enzymes that are found in all living organisms. Uracil-DNA glycosylase (EC 3.2.2.27) and EC 3.2.2.28 form a central part of the DNA-repair machinery since they initiate the DNA base-excision repair pathway by hydrolysing the N-glycosidic bond between uracil and the deoxyribose sugar thereby catalysing the removal of mis-incorporated uracil from DNA.
References: [143, 2453, 1690]

[EC 3.2.2.28 created 2009]

EC 3.2.2.29
Accepted name: thymine-DNA glycosylase
Reaction: Hydrolyses mismatched double-stranded DNA and polynucleotides, releasing free thymine.
Other name(s): hTDG; hsTDG; TDG; thymine DNA glycosylase; G/T glycosylase; uracil/thymine DNA glycosylase; G:T mismatch-specific thymidine-DNA glycosylase; T:G mismatch-specific thymine DNA-glycosylase
Systematic name: thymine-DNA deoxyribohydrolase (thymine-releasing)
Comments: Thymine-DNA glycosylase is part of the DNA-repair machinery. Thymine removal is fastest when it is from a G/T mismatch with a 5′-flanking C/G pair. The glycosylase removes uracil from G/U, C/U, and T/U base pairs faster than it removes thymine from G/T [2752].
References: [2753, 1789, 2752]

[EC 3.2.2.29 created 2009]

EC 3.2.3 Hydrolysing S-glycosyl compounds (deleted sub-subclass)
[3.2.3.1 Transferred entry. thioglucosidase. Now EC 3.2.1.147, thioglucosidase]

[EC 3.2.3.1 created 1972, deleted 2001]
EC 3.3 Acting on ether bonds

This subclass contains enzymes that act on ether bonds. It is subdivided into those hydrolysing thioether and trialkylsulfonium compounds (EC 3.3.1) and those acting on ethers (EC 3.3.2).

EC 3.3.1 Thioether and trialkylsulfonium hydrolases

EC 3.3.1.1

Accepted name: adenosylhomocysteine

Reaction: S-adenosyl-L-homocysteine + H₂O = L-homocysteine + adenosine

Other name(s): S-adenosylhomocysteine synthase; S-adenosylhomocysteine hydrolase (ambiguous); adenosylhomocysteine hydrolase; S-adenosylhomocysteine; SAHase; AdoHcyase

Systematic name: S-adenosyl-L-homocysteine hydrolase

Comments: The enzyme contains one tightly bound NAD⁺ per subunit. This appears to bring about a transient oxidation at C-3' of the 5'-deoxyadenosine residue, thus labilizing the thioether bond [1933] (for mechanism, click here), cf. EC 5.5.1.4, inositol-3-phosphate synthase.

References: [499, 1933]

[EC 3.3.1.1 created 1961, modified 2004]

EC 3.3.1.2

Accepted name: adenosylmethionine hydrolase

Reaction: S-adenosyl-L-methionine + H₂O = L-homoserine + methylthioadenosine

Other name(s): S-adenosylmethionine cleaving enzyme; methylmethionine-sulfonium-salt hydrolase; adenosylmethionine lyase

Systematic name: S-adenosyl-L-methionine hydrolase

Comments: Also hydrolyses methylmethionine sulfonium salt to dimethyl sulfide and homoserine.

References: [1608]

[EC 3.3.1.2 created 1972, modified 1976]

[3.3.1.3 Deleted entry. ribosylhomocysteinase. This enzyme was transferred to EC 3.2.1.148, ribosylhomocysteinase, which has since been deleted. The activity is most probably attributable to EC 4.4.1.21, S-ribosylhomocysteine lyase]

[EC 3.3.1.3 created 1972, deleted 2001]

EC 3.3.2 Ether hydrolases

EC 3.3.2.1

Accepted name: isochorismatase

Reaction: isochorismate + H₃O = 2,3-dihydroxy-2,3-dihydrobenzoate + pyruvate

Other name(s): 2,3-dihydro-2,3-dihydroxybenzoate synthase; 2,3-dihydroxy-2,3-dihydrobenzoate synthase; 2,3-dihydroxy-2,3-dihydrobenzoic synthase

Systematic name: isochorismate pyruvate-hydrolase

References: [2897]

[EC 3.3.2.1 created 1972]

EC 3.3.2.2

Accepted name: alkenylglycerophosphocholine hydrolase

Reaction: 1-(1-alkenyl)-sn-glycero-3-phosphocholine + H₂O = an aldehyde + sn-glycero-3-phosphocholine
Other name(s): lysoplasmalogenase
Systematic name: 1-(1-alkenyl)-sn-glycero-3-phosphocholine aldehydohydrolase
References: [70, 617, 2747]

[EC 3.3.2.2 created 1972, modified 1976]

[3.3.2.3 Transferred entry. epoxide hydrolase. Now known to comprise two enzymes, microsomal epoxide hydrolase (EC 3.3.2.9) and soluble epoxide hydrolase (EC 3.3.2.10)]

[EC 3.3.2.3 created 1978, modified 1999, deleted 2006]

EC 3.3.2.4
Accepted name: trans-epoxysuccinate hydrolase
Reaction: trans-2,3-epoxysuccinate + H₂O = meso-tartrate
trans-2,3-epoxysuccinate hydratase; tartrate epoxydase
Systematic name: trans-2,3-epoxysuccinate hydrolase
Comments: Acts on both optical isomers of the substrate.
References: [34]

[EC 3.3.2.4 created 1984]

EC 3.3.2.5
Accepted name: alkenylglycerophosphoethanolamine hydrolase
Reaction: 1-(1-alkenyl)-sn-glycero-3-phosphoethanolamine + H₂O = an aldehyde + sn-glycero-3-phosphoethanolamine
Systematic name: 1-(1-alkenyl)-sn-glycero-3-phosphoethanolamine aldehydohydrolase
References: [888]

[EC 3.3.2.5 created 1984]

EC 3.3.2.6
Accepted name: leukotriene-A₄ hydrolase
Reaction: (7E,9E,11Z,14Z)-(5S,6S)-5,6-epoxyicosa-7,9,11,14-tetraenoate + H₂O = (6Z,8E,10E,14Z)-(5S,12R)-5,12-dihydroxyicosa-6,8,10,14-tetraenoate
Other name(s): LTA₄ hydrolase; LTA4H; leukotriene A₄ hydrolase
Systematic name: (7E,9E,11Z,14Z)-(5S,6S)-5,6-epoxyicosa-7,9,11,14-tetraenoate hydrolase
Comments: This is a bifunctional zinc metalloprotease that displays both epoxide hydrolase and aminopeptidase activities [1798, 1908]. It preferentially cleaves tripeptides at an arginyln bond, with dipeptides and tetrapeptides being poorer substrates [1908] (see EC 3.4.11.6, aminopeptidase B). It also converts leukotriene A₄ into leukotriene B₄, unlike EC 3.2.2.10, soluble epoxide hydrolase, which converts leukotriene A₄ into 5,6-dihydroxy-7,9,11,14-icosatetraenoic acid [901, 1798]. In vertebrates, five epoxide-hydrolase enzymes have been identified to date: EC 3.3.2.6 (leukotriene A₄ hydrolase), EC 3.3.2.7 (hepoxilin-epoxide hydrolase), EC 3.3.2.9 (microsomal epoxide hydrolase), EC 3.3.2.10 (soluble epoxide hydrolase) and EC 3.3.2.11 (cholesterol-5,6-oxide hydrolase) [901].
References: [648, 1668, 901, 1798, 727, 1908, 1876]

[EC 3.3.2.6 created 1989, modified 2006]

EC 3.3.2.7
Accepted name: hepoxilin-epoxide hydrolase
Reaction: (5Z,9E,14Z)-(8E,11R,12S)-11,12-epoxy-8-hydroxyicosa-5,9,14-trienoate + H₂O = (5Z,9E,14Z)-(8E,11R,12S)-11,12-trihydroxyicosa-5,9,14-trienoate
Other name(s): hepoxilin epoxide hydrolase; hepoxilin hydrolase; hepoxilin A₁ hydrolase
Systematic name: (5Z,9E,14Z)-(8E,11R,12S)-11,12-epoxy-8-hydroxyicosa-5,9,14-trienoate hydrolase

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Comments: Converts hepoxilin A₃ into trioxilin A₃. Highly specific for the substrate, having only slight activity with other epoxides such as leukotriene A₄ and styrene oxide [1927]. Hepoxilin A₃ is an hydroxy-epoxide derivative of arachidonic acid that is formed via the 12-lipoxygenase pathway [1927]. It is probable that this enzyme plays a modulatory role in inflammation, vascular physiology, systemic glucose metabolism and neurological function [1798]. In vertebrates, five epoxide-hydrolase enzymes have been identified to date: EC 3.3.2.6 (leukotriene-A₄ hydrolase), EC 3.3.2.7 (hepoxilin-epoxide hydrolase), EC 3.3.2.9 (microsomal epoxide hydrolase), EC 3.3.2.10 (soluble epoxide hydrolase) and EC 3.3.2.11 (cholesterol 5,6-oxide hydrolase) [727].

References: [1926, 1927, 727, 1798]

EC 3.3.2.8

Accepted name: limonene-1,2-epoxide hydrolase
Reaction: 1,2-epoxymeth-8-ene + H₂O = menth-8-ene-1,2-diol
Other name(s): limonene oxide hydrolase; limonene-1,2-epoxide hydrolase
Systematic name: 1,2-epoxymeth-8-ene hydrolase
Comments: Involved in the monoterpene degradation pathway of the actinomycete Rhodococcus erythropolis. The enzyme hydrolyses several alicyclic and 1-methyl-substituted epoxides, such as 1-methycyclohexene oxide, indene oxide and cyclohexene oxide. It differs from the previously described epoxide hydrolases [EC 3.3.2.4 (trans-epoxysuccinate hydrolase), EC 3.3.2.6 (leukotriene-A₄ hydrolase), EC 3.3.2.7 (hepoxilin-epoxide hydrolase), EC 3.3.2.9 (microsomal epoxide hydrolase) and EC 3.3.2.10 (soluble epoxide hydrolase)] as it is not inhibited by 2-bromo-4′-nitroacetophenone, diethyl dicarbonate, 4-fluorochalcone oxide or 1,10-phenanthroline. Both enantiomers of menth-8-ene-1,2-diol [i.e. (1R,2R,4S)-menth-8-ene-1,2-diol and 1S,2S,4R)-menth-8-ene-1,2-diol] are metabolized.

References: [2672, 123, 2673]

[EC 3.3.2.8 created 2001]

EC 3.3.2.9

Accepted name: microsomal epoxide hydrolase
Reaction: cis-stilbene oxide + H₂O = (+)-(1R,2R)-1,2-diphenylethane-1,2-diol
Other name(s): epoxide hydratase (ambiguous); microsomal epoxide hydratase (ambiguous); epoxide hydrase; microsomal epoxide hydrase; arene-oxide hydratase (ambiguous); benzo[a]pyrene-4,5-oxide hydratase; benzo(a)pyrene-4,5-epoxide hydratase; aryl epoxide hydrase (ambiguous); cis-epoxide hydrolase; mEH
Systematic name: cis-stilbene-oxide hydrolase
Comments: This is a key hepatic enzyme that is involved in the metabolism of numerous xenobiotics, such as 1,3-butadiene oxide, styrene oxide and the polycyclic aromatic hydrocarbon benzo[a]pyrene 4,5-oxide [5—7]. In a series of oxiranes with a lipophilic substituent of sufficient size (styrene oxides), mono-substituted as well as 1,1- and cis-1,2-disubstituted oxiranes serve as substrates or inhibitors of the enzyme. However, trans-1,2-disubstituted, tri-and tetra-substituted oxiranes are not substrates [1373]. The reaction involves the formation of an hydroxyalkyl—enzyme intermediate [1798]. In vertebrates, five epoxide-hydrolase enzymes have been identified to date: EC 3.3.2.6 (leukotriene-A₄ hydrolase), EC 3.3.2.7 (hepoxilin-epoxide hydrolase), EC 3.3.2.9 (microsomal epoxide hydrolase), EC 3.3.2.10 (soluble epoxide hydrolase) and EC 3.3.2.11 (cholesterol 5,6-oxide hydrolase) [727].

References: [1127, 1502, 1860, 1861, 170, 1711, 727, 1859, 1373, 1798]

[EC 3.3.2.9 created 2006 (EC 3.3.2.3 part-incorporated 2006)]

EC 3.3.2.10

Accepted name: soluble epoxide hydrolase
Reaction: an epoxide + H₂O = a glycol

References: [1926, 1927, 727, 1798]

[EC 3.3.2.10 created 1992, modified 2006]
Other name(s): epoxide hydrolase (ambiguous); epoxide hydratase (ambiguous); arene-oxide hydratase (ambiguous); aryl epoxide hydrase (ambiguous); trans-stilbene oxide hydrolase; sEH; cytosolic epoxide hydrolase

Systematic name: epoxide hydrolase

Comments: Catalyses the hydrolysis of trans-substituted epoxides, such as trans-stilbene oxide, as well as various aliphatic epoxides derived from fatty-acid metabolism [727]. It is involved in the metabolism of arachidonic epoxides (epoxyicosatrienoic acids; EETs) and linoleic acid epoxides. The EETs, which are endogenous chemical mediators, act at the vascular, renal and cardiac levels to regulate blood pressure [1711, 2900]. The enzyme from mammals is a bifunctional enzyme: the C-terminal domain exhibits epoxide-hydrolase activity and the N-terminal domain has the activity of EC 3.1.3.76, lipid-phosphate phosphatase [1799, 455]. Like EC 3.3.2.9, microsomal epoxide hydrolase, it is probable that the reaction involves the formation of an hydroxyalkyl—enzyme intermediate [1711, 1372]. The enzyme can also use leukotriene A4, the substrate of EC 3.3.2.6, leukotriene-A4 hydrolase, but it forms 5,6-dihydroxy-7,9,11,14-icosatetraenoic acid rather than leukotriene B4 as the product [901, 1798]. In vertebrates, five epoxide-hydrolase enzymes have been identified to date: EC 3.3.2.6 (leukotriene-A4 hydrolase), EC 3.3.2.7 (hepoxilin-epoxide hydrolase), EC 3.3.2.9 (microsomal epoxide hydrolase), EC 3.3.2.10 (soluble epoxide hydrolase) and EC 3.3.2.11 (cholesterol 5,6-oxide hydrolase) [727].

References: [1799, 455, 1859, 1711, 2900, 1372, 727, 2909, 901, 1798]

EC 3.3.2.11

Accepted name: cholesterol-5,6-oxide hydrolase

Reaction: (1) 5,6α-epoxy-5α-cholestan-3β-ol + H2O = 5α-cholestan-3β,5α,6β-triol
(2) 5,6β-epoxy-5β-cholestan-3β-ol + H2O = 5α-cholestan-3β,5α,6β-triol

Other name(s): cholesterol-epoxide hydrolase; ChEH

Systematic name: 5,6α-epoxy-5α-cholestan-3β-ol hydrolase

Comments: The enzyme appears to work equally well with either epoxide as substrate [2283]. The product is a competitive inhibitor of the reaction. In vertebrates, five epoxide-hydrolase enzymes have been identified to date: EC 3.3.2.6 (leukotriene-A4 hydrolase), EC 3.3.2.7 (hepoxilin-epoxide hydrolase), EC 3.3.2.9 (microsomal epoxide hydrolase), EC 3.3.2.10 (soluble epoxide hydrolase) and EC 3.3.2.11 (cholesterol 5,6-oxide hydrolase) [2283].

References: [1428, 1862, 2283, 727, 1798]

EC 3.4 Acting on peptide bonds (peptidases)

It is recommended that the term "peptidase" be used as being synonymous with "peptide hydrolase" for any enzyme that hydrolyses peptide bonds. Peptidases are recommended to be further divided into "exopeptidases" that act only near a terminus of a polypeptide chain and "endopeptidases" that act internally in polypeptide chains. The types of exopeptidases and endopeptidases are described more fully below. The usage of "peptidase", which is now recommended, is synonymous with "protease" as it was originally used [1] as a general term for both exopeptidases and endopeptidases, but it should be noted that previously, in Enzyme Nomenclature (1984), "peptidase" was restricted to the enzymes included in sub-subclasses EC 3.4.11 and EC 3.4.13-19, the exopeptidases. Also, the term "protease" used previously for the enzymes included in sub-subclasses EC 3.4.21-25 carried the same meaning as "endopeptidase", and has been replaced by "endopeptidase", for consistency.

The nomenclature of the peptidases is troublesome. Their specificity is commonly difficult to define, depending upon the nature of several amino-acid residues around the peptide bond to be hydrolysed and also on the conformation of the substrate’s polypeptide chain. A classification involving the additional criterion of catalytic mechanism is therefore used.

Two sets of sub-subclasses of peptidases are recognized, those of the exopeptidases (EC 3.4.11 and EC 3.4.13-19) and those of the endopeptidases (EC 3.4.21-25). The exopeptidases act only near the ends of polypeptide chains, and those acting at a free N-terminus liberate a single amino-acid residue (aminopeptidases; EC 3.4.11), or a dipeptide or a tripeptide (dipeptidyl-peptidases and tripeptidyl-peptidases; EC 3.4.14). The endopeptidases that act at a free C-terminus liberate a single residue (carboxypeptidases, EC 3.4.16-18), or a dipeptide (peptidyl-dipeptidases; EC 3.4.15). The carboxypeptidases are allocated to
three groups on the basis of catalytic mechanism: the serine-type carboxypeptidases (EC 3.4.16), the metallocarboxypeptidases (EC 3.4.17) and the cysteine-type carboxypeptidases (EC 3.4.18). Other exopeptidases are specific for dipeptides (dipeptidases, EC 3.4.13), or for removal of terminal residues that are substituted, cyclized or linked by isopeptide bonds (peptide linkages other than those of alpha-carboxyl to alpha-amino groups) (omega peptidases; EC 3.4.19).

The endopeptidases are divided into sub-subclasses on the basis of catalytic mechanism, and specificity is used only to identify individual enzymes within the groups. The sub-subclasses are: serine endopeptidases (EC 3.4.21), cysteine endopeptidases (EC 3.4.22), aspartic endopeptidases (EC 3.4.23), metalloendopeptidases (EC 3.4.24) and threonine endopeptidases (EC 3.4.25).

There are characteristic inhibitors of the members of each catalytic type of endopeptidase; to save space, these have not been listed separately for each individual enzyme but are reviewed in [2] and [3]. A general source of information on peptidases that similarly has not been cited for each individual enzyme is reference [4].

In describing the specificity of peptidases, use is made of a model in which the catalytic site is considered to be flanked on one or both sides by specificity subsites, each able to accommodate the sidechain of a single amino-acid residue (based on [5]). These sites are numbered from the catalytic site, $S_1...S_n$ towards the N-terminus of the substrate, and $S_1'...S_n'$ towards the C-terminus. The residues they accommodate are numbered $P_1...P_n$ and $P_1'...P_n'$, respectively, as follows:

- **Substrate**: $-P_3-P_2-P_1$ $+P_1'-P_2'-P_3'$
- **Enzyme**: $-S_3-S_2-S_1$ $+S_1'-S_2'-S_3'$

In this representation, the catalytic site of the enzyme is marked by an asterisk (*). The peptide bond cleaved (the scissile bond) is indicated by the symbol ‘+’ or a hyphen in the structural formula of the substrate, or a hyphen in the name of the enzyme.

Finally, in describing the specificity of endopeptidases, the term oligopeptidase’ is used to refer to those that act optimally on substrates smaller than proteins.

Families of peptidases are referred to by use of the numbering system of Rawlings & Barrett [6,7].

**References**


**EC 3.4.1 α-Amino-acyl-peptide hydrolases (deleted sub-subclass)**

**[3.4.1.1] Transferred entry. leucyl aminopeptidase. Now EC 3.4.11.1, leucyl aminopeptidase**

EC 3.4.1.1 created 1961, deleted 1972

**[3.4.1.2] Transferred entry. aminopeptidase. Now EC 3.4.11.2, membrane alanyl aminopeptidase**

EC 3.4.1.2 created 1961, deleted 1972

**[3.4.1.3] Transferred entry. aminotripeptidase. Now EC 3.4.11.4, tripeptide aminopeptidase**

EC 3.4.1.3 created 1961, deleted 1972

**[3.4.1.4] Transferred entry. proline iminopeptidase. Now EC 3.4.11.5, prolyl aminopeptidase**

EC 3.4.1.4 created 1965, deleted 1972
EC 3.4.2 Peptidyl-amino-acid hydrolases (deleted sub-subclass)

[3.4.2.1  Transferred entry. carboxypeptidase A. Now EC 3.4.17.1, carboxypeptidase A]
[EC 3.4.2.1 created 1961, deleted 1972]

[3.4.2.2  Transferred entry. carboxypeptidase B. Now EC 3.4.17.2, carboxypeptidase B]
[EC 3.4.2.2 created 1961, deleted 1972]

[3.4.2.3  Transferred entry. yeast carboxypeptidase. Now EC 3.4.17.4, Gly-Xaa carboxypeptidase]
[EC 3.4.2.3 created 1961, deleted 1972]

EC 3.4.3 Dipeptide hydrolases (deleted sub-subclass)

[3.4.3.1  Transferred entry. glycyl-glycine dipeptidase. Now EC 3.4.13.18, cytosol nonspecific dipeptidase]
[EC 3.4.3.1 created 1961, deleted 1972]

[3.4.3.2  Transferred entry. glycyl-leucine dipeptidase. Now EC 3.4.13.18, cytosol nonspecific dipeptidase]
[EC 3.4.3.2 created 1961, deleted 1972]

[3.4.3.3  Transferred entry. aminoacyl-histidine dipeptidase. Now EC 3.4.13.3, Xaa-His dipeptidase]
[EC 3.4.3.3 created 1961, deleted 1972]

[3.4.3.4  Transferred entry. aminoacyl-methylhistidine dipeptidase. Now EC 3.4.13.5, Xaa-methyl-His dipeptidase]
[EC 3.4.3.4 created 1961, deleted 1972]

[3.4.3.5  Transferred entry. cysteinylglycine dipeptidase. Now EC 3.4.11.2, membrane alanyl aminopeptidase]
[EC 3.4.3.5 created 1961, deleted 1972]

[3.4.3.6  Transferred entry. iminodipeptidase. Now EC 3.4.13.18, cytosol nonspecific dipeptidase]
[EC 3.4.3.6 created 1961, deleted 1972]

[3.4.3.7  Transferred entry. iminodipeptidase. Now EC 3.4.13.9, Xaa-Pro dipeptidase]
[EC 3.4.3.7 created 1961, deleted 1972]

EC 3.4.4 Peptidyl peptide hydrolases (deleted sub-subclass)

[3.4.4.1  Transferred entry. pepsin. Now EC 3.4.23.1, pepsin A]
[EC 3.4.4.1 created 1961, deleted 1972]

[3.4.4.2  Transferred entry. pepsin B. Now EC 3.4.23.2, pepsin B]
[EC 3.4.4.2 created 1961, deleted 1972]

[3.4.4.3  Transferred entry. rennin. Now EC 3.4.23.4, chymosin]
[EC 3.4.4.3 created 1961, deleted 1972]

[3.4.4.4  Transferred entry. trypsin. Now EC 3.4.21.4, trypsin]
[EC 3.4.4.4 created 1961, deleted 1972]

[3.4.4.5  Transferred entry. chymotrypsin. Now EC 3.4.21.1, chymotrypsin]
[EC 3.4.4.5 created 1961, deleted 1972]

[3.4.4.6 Transferred entry. chymotrypsin B. Now EC 3.4.21.1, chymotrypsin]

[EC 3.4.4.6 created 1961, deleted 1972]

[3.4.4.7 Transferred entry. elastase. Now covered by EC 3.4.21.36, pancreatic elastase and EC 3.4.21.37, leukocyte elastase]

[EC 3.4.4.7 created 1961, deleted 1972]

[3.4.4.8 Transferred entry. enteropeptidase. Now EC 3.4.21.9, enteropeptidase]

[EC 3.4.4.8 created 1961, deleted 1972]

[3.4.4.9 Transferred entry. cathepsin C. Now EC 3.4.14.1, dipeptidyl-peptidase I]

[EC 3.4.4.9 created 1961, deleted 1972]

[3.4.4.10 Transferred entry. papain. Now EC 3.4.22.2, papain]

[EC 3.4.4.10 created 1961, deleted 1972]

[3.4.4.11 Transferred entry. chymopapain. Now EC 3.4.22.6, chymopapain]

[EC 3.4.4.11 created 1961, deleted 1972]

[3.4.4.12 Transferred entry. ficin. Now EC 3.4.22.3, ficain]

[EC 3.4.4.12 created 1961, deleted 1972]

[3.4.4.13 Transferred entry. thrombin. Now EC 3.4.21.5, thrombin]

[EC 3.4.4.13 created 1961, deleted 1972]

[3.4.4.14 Transferred entry. plasmin. Now EC 3.4.21.7, plasmin]

[EC 3.4.4.14 created 1961, deleted 1972]

[3.4.4.15 Transferred entry. renin. Now EC 3.4.23.15, renin]

[EC 3.4.4.15 created 1961, deleted 1972]

[3.4.4.16 Transferred entry. subtilopeptidase A. Now covered by the microbial serine proteinases EC 3.4.21.62 (subtilisin), EC 3.4.21.63 (oryzin), EC 3.4.21.64 (endopeptidase K), EC 3.4.21.65 (thermomycolin), EC 3.4.21.66 (thermitase) and EC 3.4.21.67 (ndopeptidase So)]

[EC 3.4.4.16 created 1961, deleted 1972]

[3.4.4.17 Transferred entry. aspergillopeptidase A. Now covered by the microbial aspartic proteinases EC 3.4.23.20 (penicillopepsin), EC 3.4.23.21 (rhizopuspepsin), EC 3.4.23.22 (endothiapepsin), EC 3.4.23.23 (mucorpepsin), EC 3.4.23.24 (candidapepsin), EC 3.4.23.25 (saccharopepsin), EC 3.4.23.26 (rhodotorulaepepsin), EC 3.4.21.103 (physarolisin), EC 3.4.23.28 (acrocylindropepsin), EC 3.4.23.29 (polyporopepsin) and EC 3.4.23.30 (pycnoporopepsin)]

[EC 3.4.4.17 created 1961, deleted 1972]

[3.4.4.18 Transferred entry. streptococcus peptidase A. Now EC 3.4.22.10, stretopain]

[EC 3.4.4.18 created 1961, deleted 1972]

[3.4.4.19 Transferred entry. clostridiopeptidase A. Now EC 3.4.24.3, microbial collagenase]

[EC 3.4.4.19 created 1961, deleted 1972]

[3.4.4.20 Transferred entry. clostridiopeptidase B. Now EC 3.4.22.8, clostripain]

[EC 3.4.4.20 created 1961, deleted 1972]

[3.4.4.21 Transferred entry. kallikrein. Now EC 3.4.21.34 (plasma kallikrein) and EC 3.4.21.35 (tissue kallikrein)]

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EC 3.4.11 Aminopeptidases

EC 3.4.11.1

Accepted name: leucyl aminopeptidase

Reaction: Release of an N-terminal amino acid, Xaa-Yaa-, in which Xaa is preferably Leu, but may be other amino acids including Pro although not Arg or Lys, and Yaa may be Pro. Amino acid amides and methyl esters are also readily hydrolysed, but rates on arylamides are exceedingly low

Other name(s): leucine aminopeptidase; leucyl peptidase; peptidase S; cytosol aminopeptidase; cathepsin III; L-leucine aminopeptidase; leucinaminopeptidase; leucinamide aminopeptidase; FTBL proteins; proteinates FTBL; aminopeptidase II; aminopeptidase III; aminopeptidase I

Comments: A zinc enzyme isolated from pig kidney and cattle lens; activated by heavy metal ions. Type example of peptidase family M17.

References: [1008, 514, 2676]

[EC 3.4.11.1 created 1961 as EC 3.4.1.1, transferred 1972 to EC 3.4.11.1]

EC 3.4.11.2

Accepted name: membrane alanyl aminopeptidase

Reaction: Release of an N-terminal amino acid, Xaa-Yaa- from a peptide, amide or arylamide. Xaa is preferably Ala, but may be most amino acids including Pro (slow action). When a terminal hydrophobic residue is followed by a prolyl residue, the two may be released as an intact Xaa-Pro dipeptide

Other name(s): microsomal aminopeptidase; aminopeptidase M; aminopeptidase N; particle-bound aminopeptidase; amino-oligopeptidase; alanine aminopeptidase; membrane aminopeptidase I; pseudo leucine aminopeptidase; alanyl aminopeptidase; alanine-specific aminopeptidase; cysteinylglycinase; cysteinylylglicinase; L-alanine aminopeptidase; CD13

Comments: A zinc enzyme, not activated by heavy metal ions. Type example of peptidase family M1.

References: [2708, 1265, 860, 2347, 679]

[EC 3.4.11.2 created 1961 as EC 3.4.1.2, transferred 1972 to EC 3.4.11.2 (EC 3.4.13.6 created 1961 as EC 3.4.3.5, transferred 1972 to EC 3.4.13.6, incorporated 1997)]

EC 3.4.11.3

Accepted name: cystinyl aminopeptidase

Reaction: Release of an N-terminal amino acid, Cys-Xaa-, in which the half-cystine residue is involved in a disulfide loop, notably in oxytocin or vasopressin. Hydrolysis rates on a range of aminoacyl arylamides exceed that for the cystinyl derivative, however [4]

Other name(s): cystyl-aminopeptidase; oxytocinase; cystine aminopeptidase; L-cystine aminopeptidase; oxytocin peptidase; vasopresssinase

[EC 3.4.4.21 created 1965, deleted 1972]

[3.4.4.22 Transferred entry. now EC 3.4.23.3, gastricsin]

[EC 3.4.4.22 created 1965, deleted 1972]

[3.4.4.23 Transferred entry. now EC 3.4.23.5, cathepsin D]

[EC 3.4.4.23 created 1965, deleted 1972]

[3.4.4.24 Transferred entry. now covered by EC 3.4.22.32 (stem bromelain) and EC 3.4.22.33 (fruit bromelain)]

[EC 3.4.4.24 created 1965, deleted 1972]

[3.4.4.25 Deleted entry. Streptomyces alkalophilic keratinase]

[EC 3.4.4.25 created 1965, deleted 1972]
Comments: A zinc-containing sialoglycoprotein in peptidase family M1 (membrane alanyl aminopeptidase family)

References: [2344, 2345, 2882, 2190]

[EC 3.4.11.3 created 1972]

EC 3.4.11.4

Accepted name: tripeptide aminopeptidase

Reaction: Release of the N-terminal residue from a tripeptide

Other name(s): tripeptidase; aminotripeptidase; aminooxotripeptidase; lymphopeptidase; imidopeptidase; peptidase B; alanine-phenylalanine-proline arylamidase; peptidase T

Comments: A zinc enzyme, widely distributed in mammalian tissues.

References: [571, 2173]

[EC 3.4.11.4 created 1961 as EC 3.4.1.3, transferred 1972 to EC 3.4.11.4]

EC 3.4.11.5

Accepted name: prolyl aminopeptidase

Reaction: Release of N-terminal proline from a peptide

Other name(s): proline aminopeptidase; Pro-X aminopeptidase; cytosol aminopeptidase V; proline iminopeptidase

Comments: A Mn\(^{2+}\)-requiring enzyme present in the cytosol of mammalian and microbial cells. In contrast to the mammalian form, the bacterial form of the enzyme (type example of peptidase family S33) hydrolyses both polypoline and prolyl-2-naphthylamide. The mammalian enzyme, which is not specific for prolyl bonds, is possibly identical with EC 3.4.11.1, leucyl aminopeptidase.

References: [2208, 1829, 2632]

[EC 3.4.11.5 created 1965 as EC 3.4.1.4, transferred 1972 to EC 3.4.11.5]

EC 3.4.11.6

Accepted name: aminopeptidase B

Reaction: Release of N-terminal Arg and Lys from oligopeptides when P1' is not Pro. Also acts on arylamides of Arg and Lys

Other name(s): arylamidase II; arginine aminopeptidase; arginyl aminopeptidase; Cl\(^-\)-activated arginine aminopeptidase; cytosol aminopeptidase IV; L-arginine aminopeptidase

Comments: Cytosolic or membrane-associated enzyme from mammalian tissues, activated by chloride ions and low concentrations of thiol compounds. This is one of the activities of the bifunctional enzyme EC 3.3.2.6 (membrane alanyl aminopeptidase family) [760, 320].

References: [773, 168, 321, 760, 320, 1908]

[EC 3.4.11.6 created 1972, modified 1997]

EC 3.4.11.7

Accepted name: glutamyl aminopeptidase

Reaction: Release of N-terminal glutamate (and to a lesser extent aspartate) from a peptide

Other name(s): aminopeptidase A; aspartate aminopeptidase; angiotensinase A; glutamyl peptidase; Ca\(^{2+}\)-activated glutamate aminopeptidase; membrane aminopeptidase II; antigen BP-1/6C3 of mouse B lymphocytes; L-aspartate aminopeptidase; angiotensinase A2

Comments: Ca\(^{2+}\)-activated and generally membrane-bound. A zinc-metallopeptidase in family M1 (membrane alanyl aminopeptidase family)

References: [824, 403, 477, 2567, 2829]

[EC 3.4.11.7 created 1972]
EC 3.4.11.9

Accepted name: Xaa-Pro aminopeptidase

Reaction: Release of any N-terminal amino acid, including proline, that is linked to proline, even from a dipeptide or tripeptide

Other name(s): proline aminopeptidase; aminopeptidase P; aminoaerylproline aminopeptidase; X-Pro aminopeptidase

Comments: A Mn$^{2+}$-dependent, generally membrane-bound enzyme present in both mammalian and bacterial cells. In peptidase family M24 (methionyl aminopeptidase family)

References: [2867, 2866, 700, 1906, 1036]

EC 3.4.11.10

Accepted name: bacterial leucyl aminopeptidase

Reaction: Release of an N-terminal amino acid, preferentially leucine, but not glutamic or aspartic acids

Other name(s): Aeromonas proteolytica aminopeptidase

Comments: A zinc enzyme. Forms of the enzyme have been isolated from Aeromonas proteolytica, Escherichia coli and Staphylococcus thermophilus. Examples are known from peptidase families M17 and M28 (of leucyl aminopeptidase and aminopeptidase Y, respectively)

References: [2019, 536, 2032]

EC 3.4.11.13

Accepted name: clostridial aminopeptidase

Reaction: Release of any N-terminal amino acid, including proline and hydroxyproline, but no cleavage of Xaa-Pro-

Other name(s): Clostridium histolyticum aminopeptidase

Comments: A secreted enzyme from Clostridium histolyticum, requiring Mn$^{2+}$ or Co$^{2+}$

References: [1239, 1240, 1241]

EC 3.4.11.14

Accepted name: cytosol alanyl aminopeptidase

Reaction: Release of an N-terminal amino acid, preferentially alanine, from a wide range of peptides, amides and arylamides

Other name(s): arylamidase; aminopolypeptidase; thiol-activated aminopeptidase; human liver aminopeptidase; puromycin-sensitive aminopeptidase; soluble alanyl aminopeptidase; cytosol aminopeptidase III; alanine aminopeptidase

Comments: A puromycin-sensitive, Co$^{2+}$-activated zinc-sialoglycoprotein that is generally cytosolic. Multiple forms are widely distributed in mammalian tissues and body fluids. In peptidase family M1 (membrane alanyl aminopeptidase family)

References: [2414, 1200, 2320]
EC 3.4.11.15
Accepted name: aminopeptidase Y
Reaction: Preferentially, release of N-terminal lysine
Other name(s): aminopeptidase Co; aminopeptidase (cobalt-activated); lysyl aminopeptidase
Comments: Requires Co\(^{2+}\); inhibited by Zn\(^{2+}\) and Mn\(^{2+}\). An enzyme best known from *Saccharomyces cerevisiae* that hydrolyses Lys-NHPhNO\(_2\) and, more slowly, Arg-NHPhNO\(_2\). Type example of peptidase family M28
References: [9, 2868, 1819]

EC 3.4.11.16
Accepted name: Xaa-Trp aminopeptidase
Reaction: Release of a variety of N-terminal residues (especially glutamate and leucine) from peptides, provided tryptophan (or at least phenylalanine or tyrosine) is the penultimate residue. Also acts on Glu-Trp, Leu-Trp and a number of other dipeptides
Other name(s): aminopeptidase W; aminopeptidase X-Trp; X-Trp aminopeptidase
Comments: A glycoprotein containing Zn\(^{2+}\), from renal and intestinal brush border membranes
References: [790, 791]

EC 3.4.11.17
Accepted name: tryptophanyl aminopeptidase
Reaction: Preferential release of N-terminal tryptophan
Other name(s): tryptophan aminopeptidase; L-tryptophan aminopeptidase
Comments: From *Trichosporon cutaneum*. Also acts on L-tryptophanamide. Requires Mn\(^{2+}\)
References: [1110]

EC 3.4.11.18
Accepted name: methionyl aminopeptidase
Reaction: Release of N-terminal amino acids, preferentially methionine, from peptides and arylamides
Other name(s): methionine aminopeptidase; peptidase M; L-methionine aminopeptidase; MAP
Comments: Membrane-bound enzyme present in both prokaryotes and eukaryotes. Type example of peptidase family M24. Releases methionine from nascent peptides
References: [2892, 2613, 722, 171, 2133]

EC 3.4.11.19
Accepted name: D-stereospecific aminopeptidase
Reaction: Release of an N-terminal D-amino acid from a peptide, Xaa—Yaa-, in which Xaa is preferably D-Ala, D-Ser or D-Thr. D-Amino acid amides and methyl esters also are hydrolysed, as is glycine amide
Other name(s): D-aminopeptidase
Comments: Known from the bacterium *Ochrobactrum anthro*. In peptidase family S12 (D-Ala-D-Ala carboxypeptidase family) [73]
References: [74, 73]
EC 3.4.11.20
Accepted name: aminopeptidase Ey
Reaction: Differs from other aminopeptidases in broad specificity for amino acids in the P1 position and the ability to hydrolyse peptides of four or five residues that contain Pro in the P1′ position
Comments: A zinc glycoprotein in peptidase family M1 (membrane alanyl aminopeptidase family), composed of two 150 kDa subunits. From the plasma fraction of hen egg yolk
References: [1071, 2515, 2514]

EC 3.4.11.21
Accepted name: aspartyl aminopeptidase
Reaction: Release of an N-terminal aspartate or glutamate from a peptide, with a preference for aspartate
Comments: Aminoacyl-arylamides are poor substrates. This is an abundant cytosolic enzyme in mammalian cells, in peptidase family M18 of aminopeptidase I
References: [1227, 2799]

EC 3.4.11.22
Accepted name: aminopeptidase I
Reaction: Release of an N-terminal amino acid, preferably a neutral or hydrophobic one, from a polypeptide. Aminoacyl-arylamides are poor substrates
Other name(s): aminopeptidase III; aminopeptidase yscI; leucine aminopeptidase IV; yeast aminopeptidase I
Comments: A 640-kDa, dodecameric enzyme best known as the major vacuolar aminopeptidase of yeast, Saccharomyces cervisiae, in which species it was first given the name aminopeptidase I (one), amongst others. Activity is stimulated by both Zn$^{2+}$ and Cl$^{-}$ ions. Type example of peptidase family M18
References: [1151, 1642, 362, 1856]

EC 3.4.11.23
Accepted name: PepB aminopeptidase
Reaction: Release of an N-terminal amino acid, Xaa, from a peptide or arylamide. Xaa is preferably Glu or Asp but may be other amino acids, including Leu, Met, His, Cys and Gln
Other name(s): Salmonella enterica serovar Typhimurium peptidase B
Comments: A 270-kDa protein composed of six 46.3-kDa subunits. The pH optimum is in the alkaline range and activity is stimulated by KCl. In peptidase family M17.
References: [1588]

EC 3.4.11.24
Accepted name: aminopeptidase S
Reaction: Release of an N-terminal amino acid with a preference for large hydrophobic amino-terminus residues
Other name(s): Mername-AA022 peptidase; SGAP; aminopeptidase (Streptomyces griseus); Streptomyces griseus aminopeptidase; S. griseus AP; double-zinc aminopeptidase
Aminopeptidases are associated with many biological functions, including protein maturation, protein degradation, cell-cycle control and hormone-level regulation [65, 768]. This enzyme contains two zinc molecules in its active site and is activated by Ca\(^{2+}\) [768]. In the presence of Ca\(^{2+}\), the best substrates are Leu-Phe, Leu-Ser, Leu-pNA (aminoacyl-p-nitroanilide), Phe-Phe-Phe and Phe-Phe [65]. Peptides with proline in the P1’ position are not substrates [65]. Belongs in peptidase family M28.

References: [2403, 172, 65, 768, 818]

EC 3.4.12 Peptidylamino-acid hydrolases or acylamino-acid hydrolases (deleted sub-subclass)

- **3.4.12.1** Transferred entry. now EC 3.4.16.5 (carboxypeptidase C) and EC 3.4.16.6 (carboxypeptidase D)
  [EC 3.4.12.1 created 1972, deleted 1978]

- **3.4.12.2** Transferred entry. now EC 3.4.17.1, carboxypeptidase A
  [EC 3.4.12.2 created 1972, deleted 1978]

- **3.4.12.3** Transferred entry. now EC 3.4.17.2, carboxypeptidase B
  [EC 3.4.12.3 created 1972, deleted 1978]

- **3.4.12.4** Transferred entry. now EC 3.4.16.2, lysosomal Pro-Xaa carboxypeptidase
  [EC 3.4.12.4 created 1972, modified 1976, deleted 1978]

- **3.4.12.5** Transferred entry. now EC 3.5.1.28, N-acetylmuramoyl-L-alanine amidase
  [EC 3.4.12.5 created 1972, deleted 1978]

- **3.4.12.6** Transferred entry. now EC 3.4.17.8, muramoyl-pentapeptidase carboxypeptidase
  [EC 3.4.12.6 created 1972, deleted 1978]

- **3.4.12.7** Transferred entry. now EC 3.4.17.3, lysine carboxypeptidase
  [EC 3.4.12.7 created 1972, deleted 1978]

- **3.4.12.8** Transferred entry. now EC 3.4.17.4, Gly-Xaa carboxypeptidase
  [EC 3.4.12.8 created 1972, deleted 1978]

- **3.4.12.9** Deleted entry. aspartate carboxypeptidase
  [EC 3.4.12.9 created 1972, deleted 1978]

- **3.4.12.10** Transferred entry. now EC 3.4.19.9, γ-glutamyl hydrolase
  [EC 3.4.12.10 created 1972, modified 1976, deleted 1978]

- **3.4.12.11** Transferred entry. now EC 3.4.17.6, alanine carboxypeptidase
  [EC 3.4.12.11 created 1972, deleted 1978]

- **3.4.12.12** Transferred entry. now EC 3.4.16.5 (carboxypeptidase C) and EC 3.4.16.6 (carboxypeptidase D)
  [EC 3.4.12.12 created 1972, deleted 1978]

- **3.4.12.13** Deleted entry. γ-glutamylglutamate carboxypeptidase
  [EC 3.4.12.13 created 1975, modified 1976, deleted 1978]

EC 3.4.13 Dipeptidases

- **3.4.13.1** Transferred entry. glycyl-glycine dipeptidase. Now EC 3.4.13.18, cytosol nonspecific dipeptidase
  [EC 3.4.13.1 created 1972, deleted 1978 [transferred to EC 3.4.13.11, deleted 1992]]

- **3.4.13.2** Transferred entry. glycyl-leucine dipeptidase. Now EC 3.4.13.18, cytosol nonspecific dipeptidase
  [EC 3.4.13.2 created 1972, deleted 1978 [transferred to EC 3.4.13.11, deleted 1992]]
EC 3.4.13.3

**Accepted name:** Xaa-His dipeptidase  
**Reaction:** Hydrolysis of Xaa-His dipeptides  
**Other name(s):** aminocacylhistidine dipeptidase; carnosinase; homocarnosinase; dipeptidase M; X-His dipeptidase  
**Comments:** A mammalian cytosolic enzyme that also acts on anserine and homocarnosine (but not on homoanserine), and to a lesser extent on some other aminocacyl-L-histidine dipeptides. Activated by thiols; inhibited by metal-chelating agents. This enzyme in peptidase family M25 may be identical with EC 3.4.13.18, cytosol nonspecific dipeptidase.  
**References:** [921, 2147, 1421, 1418]

[EC 3.4.13.3 created 1961 as EC 3.4.3.3, transferred 1972 to EC 3.4.13.3, modified 1989 (EC 3.4.13.13 created 1981, incorporated 1992)]

EC 3.4.13.4

**Accepted name:** Xaa-Arg dipeptidase  
**Reaction:** Preferential hydrolysis of Xaa-Arg, Xaa-Lys or Xaa-ornithine dipeptides  
**Other name(s):** aminoacyl-lysine dipeptidase; N\(^2\)-(4-amino-butyryl)-L-lysine hydrolase; X-Arg dipeptidase  
**Comments:** Widely distributed in mammals  
**References:** [1344]

[EC 3.4.13.4 created 1972]

EC 3.4.13.5

**Accepted name:** Xaa-methyl-His dipeptidase  
**Reaction:** Hydrolysis of anserine (β-alanyl-N\(^π\)-methyl-L-histidine), carnosine, homocarnosine, glycyl-leucine and other dipeptides with broad specificity  
**Other name(s):** anserinase; aminocacyl-methylhistidine dipeptidase; acetylhistidine deacetylase; N-acetylhistidine deacetylase; α-N-acetyl-L-histidine aminohydrolase; X-methyl-His dipeptidase  
**References:** [1159, 149, 1419]

[EC 3.4.13.5 created 1961 as EC 3.4.3.4, transferred 1972 to EC 3.4.13.5, modified 1981 (EC 3.5.1.34 created 1972, incorporated 1981)]

[3.4.13.6 Transferred entry. Cys-Gly dipeptidase. Now EC 3.4.11.2, membrane alanyl aminopeptidase]  
[EC 3.4.13.6 created 1961 as EC 3.4.3.5, transferred 1972 to EC 3.4.13.6]

EC 3.4.13.7

**Accepted name:** Glu-Glu dipeptidase  
**Reaction:** Hydrolysis of the Glu-Glu dipeptide  
**Other name(s):** α-glutamyl-glutamate dipeptidase; glutamylglutamic arylamidase  
**Comments:** It is unclear whether the specificity of this enzyme extends to other α-glutamyl dipeptides  
**References:** [2018]

[EC 3.4.13.7 created 1972]

[3.4.13.8 Transferred entry. Pro-X dipeptidase. Now EC 3.4.13.18, cytosol nonspecific dipeptidase]  
[EC 3.4.13.8 created 1961 as EC 3.4.3.6, transferred 1972 to EC 3.4.13.8]

EC 3.4.13.9

**Accepted name:** Xaa-Pro dipeptidase  
**Reaction:** Hydrolysis of Xaa-Pro dipeptides; also acts on aminocacyl-hydroxyproline analogs. No action on Pro-Pro  
**Other name(s):** prolidase; imidodipeptidase; proline dipeptidase; peptidase D; γ-peptidase; X-Pro dipeptidase  
**Comments:** A Mn\(^{2+}\)-activated enzyme, in peptidase family M24 (methionyl aminopeptidase family); cytosolic from most animal tissues.  
**References:** [489, 2348, 113, 288]
EC 3.4.13.10  Transferred entry. β-aspartyl dipeptidase. Now EC 3.4.19.5, β-aspartyl-peptidase

[EC 3.4.13.10 created 1972, deleted 1992]

EC 3.4.13.11  Transferred entry. dipeptidase. Now EC 3.4.13.19, membrane dipeptidase

[EC 3.4.13.11 created 1972, deleted 1992]

EC 3.4.13.12
Accepted name: Met-Xaa dipeptidase
Reaction: Hydrolysis of Met-Xaa dipeptidase
Other name(s): methionyl dipeptidase; dipeptidase M; Met-X dipeptidase
Comments: A Mn^{2+}-activated Escherichia coli enzyme with thiol dependence
References: [286]

[EC 3.4.13.12 created 1976]

EC 3.4.13.13  Transferred entry. homocarnosinase. Now EC 3.4.13.3, X-His dipeptidase

[EC 3.4.13.13 created 1981, deleted 1992]

EC 3.4.13.14  Deleted entry. γ-glutamyl dipeptidase

[EC 3.4.13.14 created 1989, deleted 1992]

EC 3.4.13.15  Transferred entry. N^2-β-alanylarginine dipeptidase. Now EC 3.4.13.18, cytosol nonspecific dipeptidase

[EC 3.4.13.15 created 1989, deleted 1992]

EC 3.4.13.16  Deleted entry. aspartylphenylalanine dipeptidase

[EC 3.4.13.16 created 1989, deleted 1992]

EC 3.4.13.17
Accepted name: non-stereospecific dipeptidase
Reaction: Hydrolysis of dipeptides containing either D- or L-amino acids or both
Other name(s): peptidyl-d-amino acid hydrolase; D-(or L-)aminoacyl-dipeptidase
Comments: A digestive enzyme of cephalopods
References: [476]

[EC 3.4.13.17 created 1990]

EC 3.4.13.18
Accepted name: cytosol nonspecific dipeptidase
Reaction: Hydrolysis of dipeptides, preferentially hydrophobic dipeptides including prolyl amino acids
Other name(s): N^2-β-alanylarginine dipeptidase; glycyll-glycine dipeptidase; glycyll-leucine dipeptidase; iminodipeptidase; peptidase A; Pro-X dipeptidase; prolinase; prolyl dipeptidase; prolylglycine dipeptidase; iminodipeptidase; prolinase; L-prolylglycine dipeptidase; prolylglycine dipeptidase; diglycinase; Gly-Leu hydrolase; glycyll-L-leucine dipeptidase; glycyll-L-leucine hydrolase; glycyll-L-leucine peptidase; L-aminoacyl-L-amino acid hydrolase; glycyllleucine peptidase; glycyllleucine hydrolase; glycyllleucine dipeptide hydrolase; non-specific dipeptidase; human cytosolic non-specific dipeptidase; glycyll-L-leucine hydrolase; glycyll-glycine dipeptidase
Comments: A zinc enzyme with broad specificity, varying somewhat with source species. Activated and stabilized by dithiothreitol and Mn^{2+}. Inhibited by bestatin and leucine.
References: [153]
EC 3.4.13.19
Accepted name: membrane dipeptidase
Reaction: Hydrolysis of dipeptides
Other name(s): renal dipeptidase; dehydropeptidase I (DPH I); dipeptidase; aminodipeptidase; dipeptide hydrolase; dipeptidyl hydrolase; nonspecific dipeptidase; glycosyl-phosphatidylinositol-anchored renal dipeptidase; MDP
References: [329, 330, 1334, 1037]

EC 3.4.13.20
Accepted name: β-Ala-His dipeptidase
Reaction: Preferential hydrolysis of the β-Ala-His dipeptide (carnosine), and also anserine, Xaa-His dipeptides and other dipeptides including homocarnosine
Other name(s): serum carnosinase
References: [1420, 1116]

EC 3.4.13.21
Accepted name: dipeptidase E
Reaction: Dipeptidase E catalyses the hydrolysis of dipeptides Asp-Xaa. It does not act on peptides with N-terminal Glu, Asn or Gln, nor does it cleave isoaspartyl peptides
Other name(s): aspartyl dipeptidase; peptidase E; PepE gene product (Salmonella typhimurium)
Comments: A free carboxy group is not absolutely required in the substrate since Asp-Phe-NH$_2$ and Asp-Phe-OMe are hydrolysed somewhat more slowly than dipeptides with free C-termini. No peptide larger than a C-blocked dipeptide is known to be a substrate. Asp-NH-Np is hydrolysed and is a convenient substrate for routine assay. The enzyme is most active near pH 7.0, and is not inhibited by diisopropylfluorophosphate or phenylmethanesulfonyl fluoride. Belongs in peptidase family S51.
References: [897, 1385]

EC 3.4.13.22
Accepted name: D-Ala-D-Ala dipeptidase
Reaction: D-Ala-D-Ala + H$_2$O = 2 D-Ala
Other name(s): d-alanyl-d-alanine dipeptidase; vanX D-Ala-D-Ala dipeptidase; VanX
Comments: A Zn$^{2+}$-dependent enzyme [306]. The enzyme protects Enterococcus faecium from the antibiotic vancomycin, which can bind to the -D-Ala-D-Ala sequence at the C-terminus of the peptidoglycan pentapeptide (see diagram). This enzyme reduces the availability of the free dipeptide D-Ala-D-Ala, which is the precursor for this pentapeptide sequence, allowing D-Ala-(R)-lactate (for which vancomycin has much less affinity) to be added to the cell wall instead [2832, 1610]. The enzyme is stereospecific, as L-Ala-L-Ala, D-Ala-L-Ala and L-Ala-D-Ala are not substrates [2832]. Belongs in peptidase family M15.
References: [2101, 2832, 1610, 306, 2511, 1600]
EC 3.4.14 Dipeptidyl-peptidases and tripeptidyl-peptidases

EC 3.4.14.1

**Accepted name:** dipeptidyl-peptidase I  
**Reaction:** Release of an N-terminal dipeptide, Xaa-Yaa–Zaa–, except when Xaa is Arg or Lys, or Yaa or Zaa is Pro  
**Other name(s):** cathepsin C; dipeptidyl aminopeptidase I; dipeptidyl transferase; cathepsin C; dipeptidyl transferase; dipeptide arylamidase I; DAP I  
**Comments:** A Cl⁻-dependent, lysosomal cysteine-type peptidase maximally active at acidic pH. Also polymerizes dipeptide amides, arylamides and esters at neutral pH. In peptidase family C1 (papain family).  
**References:** [1987, 1641, 1619, 1618]

[EC 3.4.14.1 created 1961 as EC 3.4.4.9, transferred 1972 to EC 3.4.14.1]

EC 3.4.14.2

**Accepted name:** dipeptidyl-peptidase II  
**Reaction:** Release of an N-terminal dipeptide, Xaa-Yaa–, preferentially when Yaa is Ala or Pro. Substrates are oligopeptides, preferentially tripeptides  
**Other name(s):** dipeptidyl aminopeptidase II; dipeptidyl arylamidase II; carboxytripeptidase; dipeptidyl peptidase II; dipeptidyl arylamidase II; DAP II; dipeptidyl(aminoo)peptidase II; dipeptidylarylaminidase  
**Comments:** A lysosomal serine-type peptidase in family S28 (Pro-X carboxypeptidase family); maximally active at acidic pH  
**References:** [1617, 1618]

[EC 3.4.14.2 created 1978]

[3.4.14.3 Transferred entry. acylamino-acid-releasing enzyme. Now EC 3.4.19.1, acylaminoacyl-peptidase]  

[EC 3.4.14.3 created 1978, deleted 1981]

EC 3.4.14.4

**Accepted name:** dipeptidyl-peptidase III  
**Reaction:** Release of an N-terminal dipeptide from a peptide comprising four or more residues, with broad specificity. Also acts on dipeptidyl 2-naphthylamides.  
**Other name(s):** dipeptidyl aminopeptidase III; dipeptidyl arylamidase III; enkephalinase B; red cell angiotensinase  
**Comments:** A cytosolic peptidase that is active at neutral pH. It has broad activity on peptides, although it is highly selective for Arg-Arg-2-naphthylamide, at pH 9.2. Active in the hydrolysis of enkephalins. A metallopeptidase, the type example of peptidase family M49.  
**References:** [1615, 759]

[EC 3.4.14.4 created 1981, modified 2001]

EC 3.4.14.5

**Accepted name:** dipeptidyl-peptidase IV  
**Reaction:** Release of an N-terminal dipeptide, Xaa-Yaa–Zaa–, from a polypeptide, preferentially when Yaa is Pro, provided Zaa is neither Pro nor hydroxyproline  
**Other name(s):** dipeptidyl aminopeptidase IV; Xaa-Pro-dipeptidyl-aminopeptidase; Gly-Pro naphthylamidase; post-proline dipeptidyl aminopeptidase IV; lymphocyte antigen CD26; glycoprotein GP110; dipeptidyl peptidase IV; glycylproline aminopeptidase; glycylproline aminopeptidase; X-prolyl dipeptidylaminopeptidase; pep X; leukocyte antigen CD26; glycylylproline dipeptidylaminopeptidase; dipeptidyl-peptide hydrolase; glycylprolyl aminopeptidase; dipeptidyl-aminopeptidase IV; DPP IV/CD26; amino acyl-prolyl dipeptidyl aminopeptidase; T cell triggering molecule Tp103; X-PDAP
A homodimer. An integral protein of the plasma membrane of lymphocytes and other mammalian cells, in peptidase family S9 (prolyl oligopeptidase family). The reaction is similar to that of the unrelated EC 3.4.14.11 Xaa-Pro dipeptidyl-peptidase of lactococci

References: [1673, 483, 1076]

[EC 3.4.14.5 created 1981, modified 1996]

EC 3.4.14.6

Accepted name: dipeptidyl-dipeptidase

Reaction: Preferential release of dipeptides from a tetrapeptide, e.g. Ala-Gly↓↓Ala-Gly. Acts more slowly on Ala-Ala↓↓Ala-Ala and Gly-Gly↑↓Gly-Gly

Other name(s): dipeptidyl tetrapeptide hydrolase; dipeptidyl ligase; tetrapeptide dipeptidase

Comments: A thiol-activated peptidase from cabbage (Brassica oleracea). Tetrapeptides are formed from Ala-Ala, Gly-Gly, Ala-Gly and Gly-Ala

References: [631]

[EC 3.4.14.6 created 1989]

[3.4.14.7 Deleted entry. tetralysine endopeptidase]

[EC 3.4.14.7 created 1989, deleted 1992]


[EC 3.4.14.8 created 1989, deleted 1992]

EC 3.4.14.9

Accepted name: tripeptidyl-peptidase I

Reaction: Release of an N-terminal tripeptide from a polypeptide, but also has endopeptidase activity.

Other name(s): tripeptidyl aminopeptidase; tripeptidyl peptidase


References: [654, 2070, 653, 1169, 1464]


EC 3.4.14.10

Accepted name: tripeptidyl-peptidase II

Reaction: Release of an N-terminal tripeptide from a polypeptide

Other name(s): tripeptidyl aminopeptidase; tripeptidyl peptidase; tripeptidyl aminopeptidase II; tripeptidyl peptidase II; TPP

Comments: A cytosolic enzyme in peptidase family S8 (subtilisin family). Active at neutral pH. Inhibited by diisopropyl fluorophosphate. Formerly included in EC 3.4.14.8

References: [116, 117, 2576]


EC 3.4.14.11

Accepted name: Xaa-Pro dipeptidyl-peptidase

Reaction: Hydrolyses Xaa-Pro↓↓ bonds to release unblocked, N-terminal dipeptides from substrates including Ala-Pro↓↓p-nitroanilide and (sequentially) Tyr-Pro↓↓Phe-Pro↓↓Gly-Pro↓↓Ile

Other name(s): X-prolyl dipeptidyl aminopeptidase; PepX; X-prolyl dipeptidyl peptidase; X-Pro dipeptidyl-peptidase

Comments: The intracellular enzyme from Lactococcus lactis (190-kDa) is the type example of peptidase family S15. The reaction is similar to that catalysed by dipeptidyl-peptidase IV of animals

References: [2911, 1646, 899, 389, 388]
EC 3.4.14.12  
**Accepted name:** Xaa-Xaa-Pro tripeptidyl-peptidase  
**Reaction:** Hydrolysis of Xaa-Xaa-Pro\[→\]Yaa- releasing the N-terminal tripeptide of a peptide with Pro as the third residue (position P1) and where Yaa is not proline  
**Other name(s):** prolyltripeptidyl amino peptidase; prolyl tripeptidyl peptidase; prolyltripeptidyl aminopeptidase; PTP-A; TPP  
**Comments:** This cell-surface-associated serine exopeptidase is found in the Gram-negative, anaerobic bacterium *Porphyromonas gingivalis*, which has been implicated in adult periodontal disease [118]. The enzyme releases the N-terminal tripeptide of peptides, such as interleukin-6. It has an absolute requirement for a proline residue at the P1 position but is completely inactivated by a proline residue at the P1′ position [118]. The size of the peptide does not affect the rate of reaction [118].  
**References:** [118, 752]

EC 3.4.15 Peptidyl-dipeptidases

EC 3.4.15.1  
**Accepted name:** peptidyl-dipeptidase A  
**Reaction:** Release of a C-terminal dipeptide, oligopeptide\[→\]Xaa-Yaa, when Xaa is not Pro, and Yaa is neither Asp nor Glu. Thus, conversion of angiotensin I to angiotensin II, with increase in vasoconstrictor activity, but no action on angiotensin II  
**Other name(s):** angiotensin I-converting enzyme; kininase II; dipeptidyl carboxypeptidase I; peptidase P; carboxy-cathepsin; dipeptidyl hydrolase; peptidyl dipeptidase; angiotensin converting enzyme; kininase II; angiotensin I-converting enzyme; carboxycathepsin; dipeptidyl carboxypeptidase; peptidyl dipeptidase I; peptidyl-dipeptidyl hydrolase; peptidyl dipeptidase hydrolase; endothelial cell peptidyl dipeptidase; ACE; peptidyl dipeptidase-4; peptidyl dipeptidase A; PDH; peptidyl dipeptidyl hydrolase; DCP  
**Comments:** A Cl\(^–\)-dependent, zinc glycoprotein that is generally membrane-bound. A potent inhibitor is captopril. Important in elevation of blood pressure, through formation of angiotensin II (vasoconstrictor) and destruction of bradykinin (vasodilator). Two molecular forms exist in mammalian tissues, a widely-distributed somatic form of 150- to 180-kDa that contains two non-identical catalytic sites, and a testicular form of 90- to 100-kDa that contains only a single catalytic site. Type example of peptidase family M2  
**References:** [2394, 611, 2766, 440]

EC 3.4.15.4  
**Accepted name:** peptidyl-dipeptidase B  
**Reaction:** Release of a C-terminal dipeptide or exceptionally a tripeptide  
**Other name(s):** dipeptidyl carboxyhydrolase; atriopeptin convertase; atrial di-(tri)peptidyl carboxyhydrolase; peptidyl dipeptidase B; atrial dipeptidyl carboxyhydrolase; atrial peptide convertase
Comments: A membrane-bound, zinc metallopeptidase located in mammalian atrial, but not ventricular, myocytes. Although it is capable of converting the 126-residue atriopeptin III directly to atriopeptin I by releasing a C-terminal tripeptide Phe-Arg-Tyr, it is generally restricted to the release of dipeptides. In contrast to peptidyl-dipeptidase A (EC 3.4.15.1) it displays no Cl\(^{-}\) dependence and shows no action on angiotensin I. Conversely, peptidyl-dipeptidase A is unable to release Phe-Arg from the C-terminus of atriopeptin II

References: [935, 936, 2379, 2380]

[EC 3.4.15 created 1992]

EC 3.4.15.5
Accepted name: peptidyl-dipeptidase Dcp
Reaction: Hydrolysis of unblocked, C-terminal dipeptides from oligopeptides, with broad specificity. Does not hydrolyse bonds in which P1' is Pro, or both P1 and P1' are Gly
Other name(s): dipeptidyl carboxypeptidase (Dcp); dipeptidyl carboxypeptidase
Comments: Known from *Escherichia coli* and *Salmonella typhimurium*. A zinc metallopeptidase in peptidase family M3 (thimet oligopeptidase family). Ac-Ala Ala-Ala is a good test substrate [426]. Inhibited by captopril, as is peptidyl-dipeptidase A. Formerly EC 3.4.15.3, and included in EC 3.4.15.1, peptidyl-dipeptidase A.
References: [2865, 985, 426]

[EC 3.4.15.5 created 1981 as EC 3.4.15.3, modified 1989, transferred 1996 to EC 3.4.15.5]

EC 3.4.15.6
Accepted name: cyanophycinase
Reaction: [L-Asp(4-L-Arg)]\(_n\) + H\(_2\)O = [L-Asp(4-L-Arg)]\(_{n-1}\) + L-Asp(4-L-Arg)
Other name(s): cyanophycin degrading enzyme; β-Asp-Arg hydrolysing enzyme; CGPase; CphB; CphE; cyanophycin granule polypeptidase; extracellular CGPase
Comments: The enzyme is highly specific for the branched polypeptide cyanophycin and does not hydrolyse poly-L-aspartate or poly-L-arginine [2110]. A serine-type exopeptidase that belongs in peptidase family S51.
References: [1845, 1846, 2110]

[EC 3.4.15.6 created 2007]

EC 3.4.16 Serine-type carboxypeptidases

[3.4.16.1] Transferred entry. serine carboxypeptidase. Now EC 3.4.16.6, carboxypeptidase D

[EC 3.4.16.1 created 1972 as EC 3.4.12.1 and EC 3.4.21.13, both transferred 1978 to EC 3.4.16.1, deleted 1993]

EC 3.4.16.2
Accepted name: lysosomal Pro-Xaa carboxypeptidase
Reaction: Cleavage of a Pro-Xaa bond to release a C-terminal amino acid
Other name(s): angiotensinase C; lysosomal carboxypeptidase C; peptidylprolylaminio acid carboxypeptidase; aminoacylproline carboxypeptidase; prolyl carboxypeptidase; carboxypeptidase P; proline-specific carboxypeptidase P; PCP; lysosomal Pro-Xaa carboxypeptidase
Comments: A lysosomal peptidase active at acidic pH that inactivates angiotensin II. Inhibited by diisopropyl fluorophosphate. In peptidase family S28 (Pro-X carboxypeptidase family).
References: [2728, 1858]

[EC 3.4.16.2 created 1972 as EC 3.4.12.4, transferred 1978 to EC 3.4.16.2]

[3.4.16.3] Transferred entry. tyrosine carboxypeptidase. Now included with EC 3.4.16.5, carboxypeptidase C]
EC 3.4.16.4

**Accepted name:** serine-type D-Ala-D-Ala carboxypeptidase  
**Reaction:** Preferential cleavage: (Ac)₂-L-Lys-D-Ala-D-Ala. Also transpeptidation of peptidyl-alanyl moieties that are N-acyl substituents of D-alanine  
**Other name(s):** DD-peptidase; D-alanyl-D-alanine-carboxypeptidase; D-alanyl-D-alanine-cleaving-peptidase; D-alanyl-D-alanine-cleaving peptidase; DD-transpeptidase; D-alanine carboxypeptidase; DD-carboxypeptidase; D-alanyl carboxypeptidase  
**Comments:** A membrane-bound, bacterial enzyme inhibited by penicillin and other β-lactam antibiotics, which acylate the active site serine. Examples are known from peptidase families S11, S12 and S13. Distinct from EC 3.4.17.14, zinc D-Ala-D-Ala carboxypeptidase  
**References:** [805, 725]

[EC 3.4.16.4 created 1989]

EC 3.4.16.5

**Accepted name:** carboxypeptidase C  
**Reaction:** Release of a C-terminal amino acid with broad specificity  
**Other name(s):** carboxypeptidase Y; serine carboxypeptidase I; cathepsin A; lysosomal protective protein; deamidase; lysosomal carboxypeptidase A; phaseolin  
**Comments:** A carboxypeptidase with optimum pH 4.5-6.0, inhibited by diisopropyl fluorophosphate, and sensitive to thiol-blocking reagents (reviewed in [261]). Widely distributed in eukaryotes. Type example of peptidase family S10.  
**References:** [261, 2661, 1113, 1660]

[EC 3.4.16.5 created 1972 as EC 3.4.12.1, transferred 1978 to EC 3.4.16.1, part transferred 1993 to EC 3.4.16.5 (EC 3.4.16.3 created 1972 as EC 3.4.12.12, transferred 1978 to EC 3.4.16.3, transferred 1992 to EC 3.4.16.1), (EC 3.4.21.13 created 1972, transferred 1978 to EC 3.4.16.1)]

EC 3.4.16.6

**Accepted name:** carboxypeptidase D  
**Reaction:** Preferential release of a C-terminal arginine or lysine residue  
**Other name(s):** cereal serine carboxypeptidase II; Saccharomyces cerevisiae KEX1 gene product; carboxypeptidase Kex1; gene KEX1 serine carboxypeptidase; KEX1 carboxypeptidase; KEX1 proteinase; KEX1DELTAp; CPDW-II; serine carboxypeptidase; Phaseolus proteinase  
**Comments:** A carboxypeptidase with optimum pH 4.5-6.0, inhibited by diisopropyl fluorophosphate, and sensitive to thiol-blocking reagents (reviewed in [261]). In peptidase family S10 (carboxypeptidase C family).  
**References:** [261, 263, 552, 1450]

[EC 3.4.16.6 created 1972 as EC 3.4.12.1, transferred 1978 to EC 3.4.16.1, part transferred 1993 to EC 3.4.16.6 (EC 3.4.16.3 created 1972 as EC 3.4.12.12, transferred 1978 to EC 3.4.16.3, transferred 1992 to EC 3.4.16.1), (EC 3.4.21.13 created 1972, transferred 1978 to EC 3.4.16.1)]

EC 3.4.17 Metallocarboxypeptidases

EC 3.4.17.1

**Accepted name:** carboxypeptidase A  
**Reaction:** Release of a C-terminal amino acid, but little or no action with -Asp, -Glu, -Arg, -Lys or -Pro  
**Other name(s):** carboxypolypeptidase; pancreatic carboxypeptidase A; tissue carboxypeptidase A  
**Comments:** A zinc enzyme formed from procarboxypeptidase A. Isolated from cattle, pig and dogfish pancreas, and other sources including mast cells [650] and skeletal muscle [299]. Type example of peptidase family M14.  
**References:** [1964, 2082, 650, 229]
EC 3.4.17.2

Accepted name: carboxypeptidase B

Reaction: Preferential release of a C-terminal lysine or arginine amino acid

Other name(s): protaminase; pancreatic carboxypeptidase B; tissue carboxypeptidase B; peptidyl-L-lysine [L-arginine]hydrolase

Comments: A zinc enzyme formed from procarboxypeptidase B. Isolated from cattle, pig and dogfish pancreas and other sources, including skin fibroblasts [309] and adrenal medulla [2724]. In peptidase family M14 (carboxypeptidase A family).

References: [705, 276, 309, 2724]

EC 3.4.17.3

Accepted name: lysine carboxypeptidase

Reaction: Release of a C-terminal basic amino acid, preferentially lysine

Other name(s): carboxypeptidase N; arginine carboxypeptidase; kininase I; anaphylatoxin inactivator; plasma carboxypeptidase B; creatine kinase conversion factor; bradykinase; kininase Ia; hippuryllysine hydrolase; bradykinin-decomposing enzyme; protaminase; CPase N; creatinine kinase convertase; peptidylL-lysine(-L-arginine) hydrolase; CPN

Comments: A zinc enzyme found in plasma. Inactivates bradykinin and anaphylatoxins in blood plasma. In peptidase family M14 (carboxypeptidase A family).

References: [1990, 1429, 2349]

EC 3.4.17.4

Accepted name: Gly-Xaa carboxypeptidase

Reaction: Release of a C-terminal amino acid from a peptide in which glycine is the penultimate amino acid, e.g. Z-Gly-Leu

Other name(s): glycine carboxypeptidase; carboxypeptidase a; carboxypeptidase S; peptidase α; yeast carboxypeptidase; Gly-X carboxypeptidase

Comments: From yeast. In peptidase family M20 (glutamate carboxypeptidase family).

References: [674, 2819]

EC 3.4.17.6

Accepted name: alanine carboxypeptidase

Reaction: Release of a C-terminal alanine from a peptide or a variety of pteroyl or acyl groups

Other name(s): N-benzyol-L-alanine-amidohydrolase

Comments: From soil bacteria. The enzyme from Corynebacterium equi also hydrolysates N-benzyolglycine and N-benzyol-L-aminobutyric acid.

References: [1452, 1679]
### 3.4.17.7 Transferred entry. acylmuramoyl-alanine carboxypeptidase. Now EC 3.5.1.28, N-acetylmuramoyl-L-alanine amidase

[EC 3.4.17.7 created 1978, deleted 1992]

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[EC 3.4.17.8 created 1972 as EC 3.4.12.6, transferred 1978 to EC 3.4.17.8]

### 3.4.17.9 Transferred entry. carboxypeptidase S. Now included with EC 3.4.17.4, Gly-Xaa carboxypeptidase

[EC 3.4.17.9 created 1981, deleted 1992]

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[EC 3.4.17.10 created 1986, modified 2000]

### 3.4.17.11

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[EC 3.4.17.11 created 1992]

### 3.4.17.12

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140
**Other name(s):** CPM  
**Comments:** A membrane-bound enzyme optimally active at neutral pH. In peptidase family M14 (carboxypeptidase A family)  
**References:** [2350, 506, 2351]

[EC 3.4.17.12 created 1992]

**EC 3.4.17.13**  
**Accepted name:** muramoyltetrapeptide carboxypeptidase  
**Reaction:** Hydrolysis of the bond: N-acetyl-D-glucosaminyl-N-acetylmuramoyl-L-Ala-D-glutamyl-6-carboxy-L-lysyl-D-alanine  
**Other name(s):** carboxypeptidase IIW; carboxypeptidase II; lysyl-D-alanine carboxypeptidase; L-lysyl-D-alanine carboxypeptidase; LD-carboxypeptidase  
**Comments:** Variants are known from various microorganisms. Involved in peptidoglycan synthesis, catalysing both decarboxylation and transpeptidation. Stimulated by divalent cations such as Mg\(^{2+}\) and Ca\(^{2+}\), but not by Zn\(^{2+}\). Inhibited by thiol-blocking reagents, but unaffected by penicillin  
**References:** [479, 2153, 1643]

[EC 3.4.17.13 created 1992]

**EC 3.4.17.14**  
**Accepted name:** zinc D-Ala-D-Ala carboxypeptidase  
**Reaction:** Cleavage of the bond: (Ac)_2-L-lysyl-D-alanyl–D-alanine  
**Other name(s):** Zn\(^{2+}\) G peptidase, D-alanyl-D-alanine hydrolase; D-alanyl-D-alanine-cleaving carboxypeptidase; DD-carboxypeptidase; G enzyme; DD-carboxypeptidase-transpeptidase  
**Comments:** A zinc enzyme. Catalyses carboxypeptidation but not transpeptidation reactions involved in bacterial cell wall metabolism. Weakly inhibited by β-lactams. In peptidase family M15. Distinct from EC 3.4.16.4, serine-type D-Ala-D-Ala carboxypeptidase.  
**References:** [538, 1161, 805]

[EC 3.4.17.14 created 1992]

**EC 3.4.17.15**  
**Accepted name:** carboxypeptidase A\(_2\)  
**Reaction:** Similar to that of carboxypeptidase A (EC 3.4.17.1), but with a preference for bulkier C-terminal residues  
**Other name(s):** CPA2  
**Comments:** Isolated from rat pancreas but not present in cattle pancreas. In peptidase family M14 (carboxypeptidase A family).  
**References:** [781]

[EC 3.4.17.15 created 1992]

**EC 3.4.17.16**  
**Accepted name:** membrane Pro-Xaa carboxypeptidase  
**Reaction:** Release of a C-terminal residue other than proline, by preferential cleavage of a prolyl bond  
**Other name(s):** carboxypeptidase P; microsomal carboxypeptidase; membrane Pro-X carboxypeptidase  
**Comments:** One of the renal brush border exopeptidases  
**References:** [509, 241, 967]

[EC 3.4.17.16 created 1992]
EC 3.4.17.17
Accepted name: tubulinyl-Tyr carboxypeptidase
Reaction: Cleavage of the -Glu→Tyr bond to release the C-terminal tyrosine residue from the native tyrosinated tubulin. Inactive on Z-Glu-Tyr
Other name(s): carboxypeptidase-tubulin; soluble carboxypeptidase; tubulin-tyrosine carboxypeptidase; tubulin-carboxypeptidase; tubulinlytyrosine carboxypeptidase; tyrosinotubulin carboxypeptidase; tyrosyltubulin carboxypeptidase; TTCPase; brain I carboxypeptidase
Comments: Active at neutral pH, from brain
References: [1748, 1341, 63]
[EC 3.4.17.17 created 1992]

EC 3.4.17.18
Accepted name: carboxypeptidase T
Reaction: Releases a C-terminal residue, which may be hydrophobic or positively charged
Other name(s): CPT
Comments: Known from Thermoactinomyces vulgaris. In peptidase family M14 (carboxypeptidase A family)
References: [1913, 2372, 2538]
[EC 3.4.17.18 created 1993]

EC 3.4.17.19
Accepted name: carboxypeptidase Taq
Reaction: Release of a C-terminal amino acid with broad specificity, except for -Pro
Comments: A 56-kDa enzyme from Thermus aquaticus. Most active at 80° C. Type example of peptidase family M32
References: [1403, 1404]
[EC 3.4.17.19 created 1996]

EC 3.4.17.20
Accepted name: carboxypeptidase U
Reaction: Release of C-terminal Arg and Lys from a polypeptide
Other name(s): arginine carboxypeptidase; carboxypeptidase R; plasma carboxypeptidase B (misleading, since the term carboxypeptidase B is used for other enzymes); thrombin-activatable fibrinolysis inhibitor
Comments: Pro-carboxypeptidase U in (human) plasma is activated by thrombin or plasmin during clotting to form the unstable carboxypeptidase U, with activity similar to that of the more stable lysine carboxypeptidase, except that no preference is shown for Lys over Arg. A zinc enzyme, in peptidase family M14 (carboxypeptidase A family)
References: [603, 2309, 2739, 2510, 289]
[EC 3.4.17.20 created 1997]

EC 3.4.17.21
Accepted name: glutamate carboxypeptidase II
Reaction: Release of an unsubstituted, C-terminal glutamyl residue, typically from Ac-Asp-Glu or folylpoly-γ-glutamates
Other name(s): N-acetylated-γ-linked-acidic dipeptidase (NAALADase); folate hydrolase; prostate-specific membrane antigen; pteroylpoly-γ-glutamate carboxypeptidase; microsomal γ-glutamyl carboxypeptidase; pteroylpolyglutamate hydrolase; folylpolyglutamate hydrolase; pteroylpoly-γ-glutamate hydrolase; pteroylpolyglutamyl hydrolase; pteroylpolyglutamate hydrolase; pteroylpolyglutamic acid hydrolase; PSM antigen; acetylaspartylglutamate dipeptidase; NAALADase; rat NAAG peptidase; mGCP; membrane glutamate carboxypeptidase; N-acetylated-α-linked-amino dipeptidase; prostate-specific membrane antigen; N-Acetylated α-linked acidic dipeptidase; PSMA
**Comments:** A metallo-carboxypeptidase that is predominantly expressed as a membrane-bound enzyme of 94-100 kDa, but also exists in a soluble form. Hydrolyses α-peptide bonds in Ac-Asp-Glu, Asp-Glu, and Glu-Glu, but also γ-glutamyl bonds in γ-Glu-Glu, and folylpoly-γ-glutamates. With folylpoly-γ-glutamates, shows processive carboxypeptidase activity to produce pteroylmonoglutamate [1515]. Does not hydrolyse Ac-β-Asp-Glu. Known inhibitors: quisqualic acid, Ac-β-Asp-Glu, and 2-phosphonomethyl-pentanedioate. In peptidase family M28 of *Vibrio* leucyl aminopeptidase. The release of C-terminal glutamate from folylpoly-γ-glutamates is also catalysed by EC 3.4.17.11 (glutamate carboxypeptidase) and EC 3.4.19.9 (γ-Glu-X carboxypeptidase).

**References:** [1001, 2069, 913, 1515]

[EC 3.4.17.21 created 1997, modified 2000 (EC 3.4.13.8 created 1972 and EC 3.4.19.8 created 1992, incorporated 2000)]

**EC 3.4.17.22**

**Accepted name:** metallocarboxypeptidase D

**Reaction:** Releases C-terminal Arg and Lys from polypeptides

**Other name(s):** carboxypeptidase D (cattle, human, mouse, rat); gp180 (duck)

**Comments:** Activated by Co$^{2+}$; inhibited by guanidinoethylmercaptosuccinic acid. Large molecule (180 kDa) because of presence of three copies of metallopeptidase domain. The product of the silver gene (*Drosophila*) is similar. A zinc metallopeptidase in peptidase family M14 (carboxypeptidase A family).

**References:** [1363, 2383, 2384]

[EC 3.4.17.22 created 1997]

**EC 3.4.17.23**

**Accepted name:** angiotensin-converting enzyme 2

**Reaction:** angiotensin II + H$_2$O $\rightarrow$ angiotensin-(1–7) + L-phenylalanine

**Other name(s):** ACE-2; ACE2; hACE2; angiotensin converting enzyme 2; angiotensin converting enzyme-2; Tmem27

**Comments:** A transmembrane glycoprotein with an extracellular catalytic domain. Angiotensin-converting enzyme 2 functions as a carboxypeptidase, cleaving a single C-terminal residue from a distinct range of substrates [1374]. Catalytic efficiency is 400-fold higher with angiotensin II (1–8) as a substrate than with angiotensin I (1–10). Angiotensin-converting enzyme 2 also efficiently hydrolyses des-Arg$^9$-bradykinin, but it does not hydrolyse bradykinin [2694]. In peptidase family M2.

**References:** [2694, 1374, 2588]

[EC 3.4.17.23 created 2009]

**EC 3.4.18 Cysteine-type carboxypeptidases**

**EC 3.4.18.1**

**Accepted name:** cathepsin X

**Reaction:** Release of C-terminal amino acid residues with broad specificity, but lacks action on C-terminal proline. Shows weak endopeptidase activity

**Other name(s):** cathepsin B2; cysteine-type carboxypeptidase; cathepsin IV; cathepsin Z; acid carboxypeptidase; lysosomal carboxypeptidase B

**Comments:** Cathepsin X is a lysosomal cysteine peptidase of family C1 (papain family). The pH optimum is dependent on the substrate and is 5.0 for the carboxypeptidase activity. Unstable above pH 7.0. Compound E-64, leupeptin and antipain are inhibitors, but not cystatin C. Cathepsin X is ubiquitously distributed in mammalian tissues. The propeptide is extremely short (38 amino acid residues) and the proenzyme is catalytically active. Human gene locus: 20q13.

**References:** [1756, 1755, 2205, 1616, 1921, 1812]

[EC 3.4.18.1 created 1981, modified 2000]
**EC 3.4.19 Omega peptidases**

**EC 3.4.19.1**

**Accepted name:** acylaminoacyl-peptidase  
**Reaction:** Cleavage of an N-acetyl or N-formyl amino acid from the N-terminus of a polypeptide  
**Other name(s):** acylamino-acid-releasing enzyme; N-acylpeptide hydrolase; N-formylmethionine (fMet) aminopeptidase; α-N-acylpeptide hydrolase  
**Comments:** Active at neutral pH. Several variants of this enzyme exist; the human erythrocyte enzyme is relatively specific for removal of N-acetylalanine from peptides. Displays dipeptidyl-peptidase activity on glycyl-peptides, perhaps as a result of mis-recognition of the glycyl residue as an uncharged N-acyl group. Inhibited by diisopropyl fluorophosphate. In peptidase family S9 (prolyl oligopeptidase family).  
**References:** [2614, 2643, 1292]

[EC 3.4.19.1 created 1978 as EC 3.4.14.3, transferred 1981 to EC 3.4.19.1]

**EC 3.4.19.2**

**Accepted name:** peptidyl-glycinamidase  
**Reaction:** Cleavage of C-terminal glycinamide from polypeptides  
**Other name(s):** carboxyamidase; peptidyl carboxy-amidase; peptidyl-aminoacylamidase; carboxamidopeptidase; peptidyl amino acid amide hydrolase  
**Comments:** Inactivates vasopressin and oxytocin by splitting off glycinamide. Also cleaves ester substrates of trypsin and chymotrypsin. Although glycinamide is by far the preferred leaving group, other aminoaoylamides may also be released, e.g. phenylalaninamide. The toad skin enzyme is inhibited by diisopropyl fluorophosphate.  
**References:** [740, 1784, 2333]

[EC 3.4.19.2 created 1978 as EC 3.4.15.2, transferred 1981 to EC 3.4.19.2]

**EC 3.4.19.3**

**Accepted name:** pyroglutamyl-peptidase I  
**Reaction:** Release of an N-terminal pyroglutamyl group from a polypeptide, the second amino acid generally not being Pro  
**Other name(s):** 5-oxoprolyl-peptidase; pyrase; pyroglutamate aminopeptidase; pyroglutamyl aminopeptidase; L-pyroglutamyl peptide hydrolase; pyrrolidone-carboxyl peptidase; pyrrolidone-carboxylate peptidase; pyrrolidonyl peptidase; L-pyrrolidonecarboxylate peptidase; pyrrolidinamidase; pyrrolidonecarboxyl peptidase  
**Comments:** A cysteine peptidase, known from bacteria, plants and animals. The enzyme from bacterial sources is used in protein sequencing, and is the type example of peptidase family C15.  
**References:** [2616, 92, 1947, 2213]

[EC 3.4.19.3 created 1972 as EC 3.4.11.8, transferred 1981 to EC 3.4.19.3, modified 1997]

**[3.4.19.4 Deleted entry. N-acetylmethionylpeptide peptidase]**

[EC 3.4.19.4 created 1989, deleted 1992]

**EC 3.4.19.5**

**Accepted name:** β-aspartyl-peptidase  
**Reaction:** Cleavage of a β-linked Asp residue from the N-terminus of a polypeptide  
**Other name(s):** β-aspartyl dipeptidase; β-aspartyl peptidase; β-aspartyldipeptidase  
**Comments:** Other isopeptide bonds, e.g. γ-glutamyl and β-alanyl, are not hydrolysed. A mammalian, cytosolic enzyme.  
**References:** [907]
EC 3.4.19.6

Accepted name: pyroglutamyl-peptidase II

Reaction: Release of the N-terminal pyroglutamyl group from pGlu-His-Xaa tripeptides and pGlu-His-Xaa-Gly tetrapeptides

Other name(s): thyroliberinase; pyroglutamyl aminopeptidase II; thyrotropin-releasing factor pyroglutamate aminopeptidase; pyroglutamylpeptidase II; thyrotropin-releasing hormone-degrading pyroglutamate aminopeptidase; thyrotropin-releasing hormone-degrading peptidase; TRH aminopeptidase


References: [154, 1847, 2800]

EC 3.4.19.7

Accepted name: N-formylmethionyl-peptidase

Reaction: Release of an N-terminal, formyl-methionyl residue from a polypeptide

Other name(s): (fMet)-releasing enzyme; formylmethionine aminopeptidase

Comments: Highly specific for N-formylmethionyl peptides. Will not cleave methionyl peptides or N-formyl derivatives of amino acids other than methionine. Isolated from rat liver. Inhibited by heavy metals and activated by Cl⁻

References: [2438]

EC 3.4.19.9

Accepted name: γ-glutamyl hydrolase

Reaction: Hydrolysis of a γ-glutamyl bond

Other name(s): conjugase; folate conjugase; lysozymal γ-glutamyl carboxypeptidase; γ-Glu-X carboxypeptidase; pteroyl-poly-γ-glutamate hydrolase; carboxypeptidase G; folic acid conjugase; poly(γ-glutamic acid) endohydrolase; polyglutamate hydrolase; poly(glutamic acid) hydrolase II; pteroyl-poly-γ-glutamyl hydrolase

Comments: A lysosomal or secreted, thiol-dependent peptidase, most active at acidic pH. Commonly studied with poly-L-glutamate as substrate, with which the initial cleavage may release glutamate or poly-γ-glutamate of two or more residues, according to the species of origin of the enzyme. Final products are pteroyl-α-glutamate (folic acid) and free glutamate. Highly specific for the γ-glutamyl bond, but not for the C-terminal amino acid (leaving group). Action on γ-glutamyl bonds is independent of an N-terminal γ-Glu residue. Inactivated by metal chelators. Type example of peptidase family C26.

References: [1622, 2741, 2862, 2863, 2861]

EC 3.4.19.10

Accepted name: acylmuramoyl-Ala peptidase. Now EC 3.5.1.28, N-acetylmuramoyl-L-alanine amidase

References: [1622, 2741, 2862, 2863, 2861]

EC 3.4.19.11
Accepted name: γ-D-glutamyl-meso-diaminopimelate peptidase

Reaction: Hydrolysis of γ-D-glutamyl bonds to the L-terminus (position 7) of meso-diaminopimelic acid (meso-A2pm) in 7-(L-Ala-γ-D-Glu)-meso-A2pm and 7-(L-Ala-γ-D-Glu)-7-(D-Ala)-meso-A2pm. It is required that the D-terminal amino and carboxy groups of meso-A2pm are unsubstituted.

Other name(s): endopeptidase I; γ-D-glutamyl-diaminopimelate endopeptidase; γ-D-glutamyl-L-meso-diaminopimelate peptidoglycan hydrolase; γ-D-glutamyl-meso-diaminopimelate endopeptidase; γ-D-glutamyl-meso-diaminopimelic acid peptidoglycan hydrolase; γ-D-glutamyl-meso-diaminopimelic endopeptidase

Comments: A 45-kDa metalloendopeptidase from Bacillus sphaericus, the substrates being components of the bacterial spore wall. A member of peptidase family M14 (carboxypeptidase A family). Endopeptidase II has similar activity, but differs in cellular location, molecular mass and catalytic mechanism [1046].

References: [67, 783, 1046]

[EC 3.4.19.11 created 1996]

EC 3.4.19.12

Accepted name: ubiquitinyl hydrolase 1

Reaction: Thiol-dependent hydrolysis of ester, thioester, amide, peptide and isopeptide bonds formed by the C-terminal Gly of ubiquitin (a 76-residue protein attached to proteins as an intracellular targeting signal)

Other name(s): ubiquitin C-terminal hydrolase; yeast ubiquitin hydrolase

Comments: Links to polypeptides smaller than 60 residues are hydrolysed more readily than those to larger polypeptides. Isoforms exist with quantitatively different specificities, amongst the best known being UCH-L1 and UCH-L3, which are major proteins of the brain of mammals [1154]. Inhibited by ubiquitin aldehyde (in which Gly76 is replaced by aminoacetaldehyde). Ubiquitinyl hydrolase 1 is the type example of peptide family C12, with a similar protein fold to papain and catalytic amino acids Cys, His and Asp. There is a separate family (C19) of enzymes that also hydrolyse ubiquitinyl bonds, and it is thought that all the ubiquitinyl hydrolases are also ubiquitin thiolesterases (EC 3.1.2.15)

References: [1154, 2803]

[EC 3.4.19.12 created 2000]

EC 3.4.21 Serine endopeptidases

EC 3.4.21.1

Accepted name: chymotrypsin

Reaction: Preferential cleavage: Tyr, Trp, Phe, Leu

Other name(s): chymotrypsins A and B; α-chymotrypsin; avazyme; chymotest; enzeon; quimar; quimotrase; α-chymotrypsin; α-chymotrypsin A; α-chymotrypsin

Comments: Chymotrypsin A is formed from cattle and pig chymotrypsinogen A, several iso-forms being produced according to the number of bonds hydrolysed in the precursor. Chymotrypsin B (formerly listed as EC 3.4.4.6), formed from chymotrypsinogen B, is homologous with chymotrypsin A. Enzymes with specificity similar to that of chymotrypsins A and B have been isolated from many species. In peptidase family S1 (trypsin family)

References: [2797, 224, 152, 1997, 2574]

[EC 3.4.21.1 created 1961 as EC 3.4.4.5 and EC 3.4.4.6, transferred 1972 to EC 3.4.21.1]

EC 3.4.21.2

Accepted name: chymotrypsin C

Reaction: Preferential cleavage: Leu, Tyr, Phe, Met, Trp, Gln, Asn

Comments: Formed from pig chymotrypsinogen C, and from cattle subunit II of procarboxypeptidase A. Reacts more readily with Tos-Leu-CH₂Cl than Tos-Phe-CH₂Cl in contrast to chymotrypsin. In peptidase family S1 (trypsin family)

References: [152, 1997, 2574, 2797]

[EC 3.4.21.2 created 1961 as EC 3.4.4.5 and EC 3.4.4.6, transferred 1972 to EC 3.4.21.1]
### EC 3.4.21.3

**Accepted name:** metridin  
**Reaction:** Preferential cleavage: Leu↓↓, Tyr↓↓, Phe↓↓, Met↓↓, Trp↓↓, Gln↓↓, Asn↓↓  
**Other name(s):** Metridium proteinase A; sea anemone protease A; sea anemone proteinase A  
**Comments:** Digestive enzyme from the sea anemone *Metridium senile.*  
**References:** [1952, 706, 2797]

### EC 3.4.21.4

**Accepted name:** trypsin  
**Reaction:** Preferential cleavage: Arg↓↓, Lys↓↓  
**Other name(s):** α-trypsin; β-trypsin; cocoonase; parenzyme; parenzymol; tryptar; trypure; pseudotrypsin; tryphtase; tripcellim; sperm receptor hydrolase  
**Comments:** The single polypeptide chain cattle β-trypsin is formed from trypsinogen by cleavage of one peptide bond. Further peptide bond cleavages produce α and other iso-forms. Isolated as multiple cationic and anionic trypsins [701] from the pancreas of many vertebrates and from lower species including crayfish, insects (cocoonase) and microorganisms (*Streptomyces griseus*) [2076]. Type example of peptidase family S1.  
**References:** [1058, 2726, 2076, 681, 701, 1997, 2523]

### EC 3.4.21.5

**Accepted name:** thrombin  
**Reaction:** Selective cleavage of Arg↓↓Gly bonds in fibrinogen to form fibrin and release fibrinopeptides A and B  
**Other name(s):** fibrinogenase; thrombase; thrombofort; topical; thrombin-C; tropestasins; activated blood-coagulation factor II; blood-coagulation factor Ila; factor Ila; E thrombin; β-thrombin; γ-thrombin  
**Comments:** Formed from prothrombin. More selective than trypsin and plasmin. In peptidase family S1 (trypsin family).  
**References:** [155, 1527, 1661, 1510, 1554, 486, 396, 1519]

### EC 3.4.21.6

**Accepted name:** coagulation factor Xa  
**Reaction:** Selective cleavage of Arg↓↓Thr and then Arg↓↓Ile bonds in prothrombin to form thrombin  
**Other name(s):** thrombokinase; prothrombase; prothrombinase; activated blood-coagulation factor X; autoprothrombin C; thromboplastin; plasma thromboplastin; factor Xa; activated Stuart-Prower factor; activated factor X  
**Comments:** Formed from the proenzyme factor X by limited proteolysis. In peptidase family S1 (trypsin family). Scutelarin (EC 3.4.21.60) has similar specificity  
**References:** [748, 1142, 486, 1115, 1623, 396]

### EC 3.4.21.7
Accepted name: plasmin
Reaction: Selective cleavage of Arg—Thr and then Arg—Ile bonds in prothrombin to form thrombin
Other name(s): fibrinase; fibrinolysin; actase; serum tryptase; thrombolysin
Comments: Formed from plasminogen by proteolysis which results in multiple forms of the active plasmin. In peptidase family S1 (trypsin family).
References: [347, 346, 2120]

[EC 3.4.21.7 created 1961 as EC 3.4.4.14, transferred 1972 to EC 3.4.21.7]

[3.4.21.8] Transferred entry. kallikrein. Now EC 3.4.21.34 (plasma kallikrein) and EC 3.4.21.35 (tissue kallikrein)

[EC 3.4.21.8 created 1972, deleted 1981]

EC 3.4.21.9
Accepted name: enteropeptidase
Reaction: Activation of trypsinogen by selective cleavage of Lys6—Ile bond
Other name(s): enterokinase
Comments: Is not inhibited by protein inhibitors of trypsin. In peptidase family S1 (trypsin family).
References: [1457]

[EC 3.4.21.9 created 1961 as EC 3.4.4.8, transferred 1972 to EC 3.4.21.9]

EC 3.4.21.10
Accepted name: acrosin
Reaction: Preferential cleavage: Arg—, Lys—
Other name(s): acrosomal proteinase; acrozonase; α-acrosin; β-acrosin; upsilon-acrosin; acrosomal protease; acrosin amidase
Comments: Occurs in spermatozoa; formed from proacrosin by limited proteolysis. Inhibited by naturally occurring trypsin inhibitors. In peptidase family S1 (trypsin family)
References: [1733, 2352, 1224]

[EC 3.4.21.10 created 1972]


[EC 3.4.21.11 created 1972, deleted 1981]

EC 3.4.21.12
Accepted name: α-lytic endopeptidase
Reaction: Preferential cleavage: Ala—, Val— in bacterial cell walls, elastin and other proteins
Other name(s): myxobacter α-lytic proteinase; α-lytic proteinase; α-lytic protease; Mycobacterium sorangium α-lytic proteinase; Myxobacter 495 α-lytic proteinase; α-lytic proteinase; Myxobacter α-lytic proteinase; Mycobacterium sorangium α-lytic proteinase
Comments: From the myxobacterium Lysobacter enzymogenes. In peptidase family S1 (trypsin family)
References: [1901, 1997, 633, 240]

[EC 3.4.21.12 created 1972]


[EC 3.4.21.13 created 1972, deleted 1978]

[3.4.21.14] Transferred entry. now EC 3.4.21.67 endopeptidase So


EC 3.4.21.19
Accepted name: glutamyl endopeptidase
Reaction: Preferential cleavage: Glu→, Asp→
Other name(s): V8 proteinase; endoproteinase Glu-C; staphylococcal serine proteinase
Comments: From Staphylococcus aureus strain V8. In appropriate buffer the specificity is restricted to Glu→. In peptidase family S1 (trypsin family)
References: [576, 578, 341]

EC 3.4.21.20
Accepted name: cathepsin G
Reaction: Specificity similar to chymotrypsin C
Other name(s): chymotrypsin-like proteinase; neutral proteinase
Comments: From azurophil granules of polymorphonuclear leukocytes. In peptidase family S1 (trypsin family)
References: [137, 2519, 1024]

EC 3.4.21.21
Accepted name: coagulation factor VIIa
Reaction: Selective cleavage of Arg→Ile bond in factor X to form factor Xa
Other name(s): blood-coagulation factor VIIa; activated blood coagulation factor VII
Comments: Formed from the precursor factor VII. The cattle enzyme is more readily inhibited by diisopropyl fluorophosphosphate than the human [1795]. In peptidase family S1 (trypsin family)
References: [1795, 486, 1115, 290]

EC 3.4.21.22
Accepted name: coagulation factor IXa
Reaction: Selective cleavage of Arg→Ile bond in factor X to form factor Xa
Other name(s): activated Christmas factor; blood-coagulation factor IXa; activated blood-coagulation factor IX; antiproteinase II; blood platelet cofactor II; activated blood coagulation factor XI
Comments: A chymotrypsin homologue, and one of the γ-carboxyglutamic acid-containing blood coagulation factors. The proenzyme factor IX is activated by factor XIa. In peptidase family S1 (trypsin family)
References: [747, 486, 1474, 396]

EC 3.4.21.23
Deleted entry. Vipera russelli proteinase
EC 3.4.21.25
Accepted name: cucumisin
Reaction: Hydrolysis of proteins with broad specificity
Comments: From the sarcocarp of the musk melon (Cucumis melo). In peptidase family S8 (subtilisin family). Other endopeptidases from plants, which are less well characterized but presumably of serine-type, include euphorbain from Euphorbia cerifera [1516], solanain from horse-nettle Solanum elaeagnifolium [865], hurain from Hura crepitans [1122] and tabernamontain from Tabernamontana grandi-flora [1121].
References: [865, 1122, 1121, 1194, 1193, 1516, 1195]

EC 3.4.21.26
Accepted name: prolyl oligopeptidase
Reaction: Hydrolysis of —Pro and to a lesser extent —Ala in oligopeptides
Other name(s): post-proline cleaving enzyme; proline-specific endopeptidase; post-proline endopeptidase; proline endopeptidase; endopropholytpidase; prolyl endopeptidase
Comments: Found in vertebrates, plants and Flavobacterium. Generally cytosolic, commonly activated by thiol compounds. Type example of peptidase family S9.
References: [2729, 1825, 1712, 2096]

EC 3.4.21.27
Accepted name: coagulation factor XIa
Reaction: Selective cleavage of Arg-Ala and Arg-Val bonds in factor IX to form factor IXa
Other name(s): blood-coagulation factor XIa; activated blood-coagulation factor XI; activated plasma thromboplatin antecedent
Comments: In peptidase family S1 (trypsin family), and one of the γ-carboxyglutamic acid-containing blood coagulation factors. The proenzyme factor XI is activated by factor XIIa
References: [1354, 396, 746]

EC 3.4.21.28
Accepted name: Agkistrodon serine proteinase. Now EC 3.4.21.74, venombin A
Reaction: selective cleavage of Arg-Ala and Arg-Val bonds in factor IX to form factor IXa
Other name(s): blood-coagulation factor XIa; activated blood-coagulation factor XI; activated plasma thromboplatin antecedent
Comments: In peptidase family S1 (trypsin family), and one of the γ-carboxyglutamic acid-containing blood coagulation factors. The proenzyme factor XI is activated by factor XIIa
References: [1354, 396, 746]

EC 3.4.21.29
Accepted name: Bothrops atrox serine proteinase. Now EC 3.4.21.74, venombin A
Reaction: selective cleavage of Arg-Ala and Arg-Val bonds in factor IX to form factor IXa
Other name(s): blood-coagulation factor XIa; activated blood-coagulation factor XI; activated plasma thromboplatin antecedent
Comments: In peptidase family S1 (trypsin family), and one of the γ-carboxyglutamic acid-containing blood coagulation factors. The proenzyme factor XI is activated by factor XIIa
References: [1354, 396, 746]

EC 3.4.21.30
Accepted name: Crotalus adamanteus serine proteinase. Now EC 3.4.21.74, venombin A
Reaction: selective cleavage of Arg-Ala and Arg-Val bonds in factor IX to form factor IXa
Other name(s): blood-coagulation factor XIa; activated blood-coagulation factor XI; activated plasma thromboplatin antecedent
Comments: In peptidase family S1 (trypsin family), and one of the γ-carboxyglutamic acid-containing blood coagulation factors. The proenzyme factor XI is activated by factor XIIa
References: [1354, 396, 746]

EC 3.4.21.31
Accepted name: urokinase. Now EC 3.4.21.73, u-plasminogen activator
Reaction: selective cleavage of Arg-Ala and Arg-Val bonds in factor IX to form factor IXa
Other name(s): blood-coagulation factor XIa; activated blood-coagulation factor XI; activated plasma thromboplatin antecedent
Comments: In peptidase family S1 (trypsin family), and one of the γ-carboxyglutamic acid-containing blood coagulation factors. The proenzyme factor XI is activated by factor XIIa
References: [1354, 396, 746]
EC 3.4.21.32

Accepted name: brachyurin

Reaction: Hydrolysis of proteins, with broad specificity for peptide bonds. Native collagen is cleaved about 75% of the length of the molecule from the N-terminus. Low activity on small molecule substrates of both trypsin and chymotrypsin

Other name(s): Uca pugilator collagenolytic proteinase; crab protease I; crab protease II

Comments: From hepatopancreas of the fiddler crab, Uca pugilator. In peptidase family S1 (trypsin family). Other serine endopeptidases that degrade collagen, but are not listed separately here, include a second endopeptidase from Uca pugilator [2777], digestive enzymes from other decapod crustacea [1282, 1503], and an enzyme from the fungus Entomophthora coronata [1062].

References: [1062, 857, 2778, 2777, 1282, 1503]

[EC 3.4.21.32 created 1978]

EC 3.4.21.33

Deleted entry. Entomophthora collagenolytic proteinase

[EC 3.4.21.33 created 1978, deleted 1992]

EC 3.4.21.34

Accepted name: plasma kallikrein

Reaction: Selective cleavage of some Arg and Lys bonds, including Lys-Arg and Arg-Ser in (human) kininogen to release bradykinin

Other name(s): serum kallikrein; kininogenase; kallikrein I; kallikrein II; kallikrein; callicrein; glumorin; padreatin; padutin; kallidinogenase; bradykininogenase; panecatic kallikrein; onokrein P; dilminal D; depot-Padutin; urokallikrein; urinary kallikrein

Comments: Formed from plasma prokallikrein (Fletcher factor) by factor XIIa. Activates coagulation factors XII, VII and plasminogen. Selective for Arg > Lys in P1, in small molecule substrates.

References: [969, 1626, 2330, 2275, 2606]

[EC 3.4.21.34 created 1965 as EC 3.4.4.21, transferred 1972 to 3.4.21.8, part transferred 1981 to EC 3.4.21.34]

EC 3.4.21.35

Accepted name: tissue kallikrein

Reaction: Preferential cleavage of Arg bonds in small molecule substrates. Highly selective action to release kallidin (lysyl-bradykinin) from kininogen involves hydrolysis of Met or Leu. The rat enzyme is unusual in liberating bradykinin directly from autoologous kininogens by cleavage at two Arg bonds [5]

Other name(s): glandular kallikrein; pancreatic kallikrein; submandibular kallikrein; submaxillary kallikrein; kidney kallikrein; urinary kallikrein; kallikrein; salivary kallikrein; kininogen; kininogenase; callicrein; glumorin; padreatin; padutin; kallidinogenase; bradykininogenase; depot-padutin; urokallikrein; dilminal D; onokrein P

Comments: Formed from tissue prokallikrein by activation with trypsin. In peptidase family S1 (trypsin family). A large number of tissue kallikrein-related sequences have been reported for rats [2808] and mice [647], though fewer seem to exist in other mammals. The few that have been isolated and tested on substrates include mouse γ-renin (EC 3.4.21.54), submandibular proteinase A [56, 185], epidermal growth-factor-binding protein, nerve growth factor γ-subunit, rat tonin [3,4,9], submaxillary proteinases A and B [1212], T-kininogenase [2835], kallikreins K7 and K8 [620] and human prostate-specific antigen (γ-semiprotein, [25])

References: [682, 56, 1960, 894, 1211, 25, 647, 681, 753, 1212, 105, 204, 364, 794, 185, 2808, 620, 2835]

[EC 3.4.21.35 created 1965 as EC 3.4.4.21, transferred 1972 to 3.4.21.8, part transferred 1981 to EC 3.4.21.35]

EC 3.4.21.36

Accepted name: pancreatic elastase
Reaction: Hydrolysis of proteins, including elastin. Preferential cleavage: Ala
Other name(s): pancreatopeptidase E; pancreatic elastase I; elastase; elaszym; serine elastase
Comments: Formed by activation of proelastase from mammalian pancreas by trypsin. In peptidase family S1 (trypsin family). Formerly included in EC 3.4.21.11
References: [2313, 933, 1219, 192, 228]

[EC 3.4.21.36 created 1981 (EC 3.4.4.7 created 1961, transferred 1972 to EC 3.4.21.11 created 1972, part incorporated 1984)]

EC 3.4.21.37
Accepted name: leukocyte elastase
Reaction: Hydrolysis of proteins, including elastin. Preferential cleavage Val→Ala
Other name(s): lysosomal elastase; neutrophil elastase; polymorphonuclear leukocyte elastase; elastase; elaszym; serine elastase; lysosomal elastase; granulocyte elastase
Comments: Differs from pancreatic elastase in specificity on synthetic substrates and in inhibitor sensitivity. In peptidase family S1 (trypsin family). Formerly included in EC 3.4.21.11
References: [138, 933, 2417, 228]

[EC 3.4.21.37 created 1981 (EC 3.4.4.7 created 1961, transferred 1972 to EC 3.4.21.11 created 1972, part incorporated 1984)]

EC 3.4.21.38
Accepted name: coagulation factor XIIa
Reaction: Selective cleavage of Arg→Ile bonds in factor VII to form factor VIIa and factor XI to form factor XIa
Other name(s): Hageman factor (activated); blood-coagulation factor XIIIf; activated β blood-coagulation factor XII; prealbumin activator; Hageman factor β-fragment; Hageman factor fragment HFa; blood-coagulation factor XIIaβ; prekallikrein activator; kallikreinogen activator
Comments: Also activates plasminogen and plasma prokallikrein. Formed from the proenzyme, factor XII, by plasma kallikrein or factor XIIa. In peptidase family S1 (trypsin family)
References: [749, 396, 2029, 745, 2329]

[EC 3.4.21.38 created 1981]

EC 3.4.21.39
Accepted name: chymase
Reaction: Preferential cleavage: Phe→Tyr→Trp→Leu
Other name(s): mast cell protease I; skeletal muscle protease; skin chymotryptic proteinase; mast cell serine proteinase, chymase; skeletal muscle (SK) protease
Comments: In mast cell granules. In peptidase family S1 (trypsin family)
References: [2823, 2016, 1148]

[EC 3.4.21.39 created 1981]

[3.4.21.40 Deleted entry. submandibular proteinase A]

[EC 3.4.21.40 created 1981, deleted 1992]

EC 3.4.21.41
Accepted name: complement subcomponent C1r
Reaction: Selective cleavage of Lys(or Arg)→Ile bond in complement subcomponent C1s to form C1rβ (EC 3.4.21.42)
Other name(s): activated complement C1r; C1rβ esterase; activated complement C1r
Comments: Activated from proenzyme C1r in plasma during activation of the complement system by the "classical" route. In peptidase family S1 (trypsin family)
References: [2331, 1436, 1732]
EC 3.4.21.42

Accepted name: complement subcomponent C1r

Reaction: Cleavage of Arg→Ala bond in complement component C4 to form C4a and C4b, and Lys(or Arg)→Lys bond in complement component C2 to form C2a and C2b: the “classical” pathway C3 convertase

Other name(s): C1 esterase; activated complement C1s; complement C1

Comments: Activated from proenzyme C1s in plasma by complement subcomponent C1r. In peptidase family S1 (trypsin family)

References: [2331, 1522, 1732, 2352]

EC 3.4.21.43

Accepted name: classical-complement-pathway C3/C5 convertase

Reaction: Selective cleavage of Arg→Ser bond in complement component C3 α-chain to form C3a and C3b, and Arg→ bond in complement component C5 α-chain to form C5a and C5b

Other name(s): C3 convertase; C11; C4b,2a; C5 convertase; C11; C4b,2a,3b; C42; C5 convertase; C423; C4b,2a,3b; complement C11; complement C11; complement C3 convertase

Comments: A complex of complement fragments C4b, C2a and C2b. C2a contains the active site, C2b the site for C4b binding. C2a and C2b are formed by cleavage of proenzyme C2 by complement subcomponent C1r. Cleavage of C5 requires complement fragment C3b which binds C5 and renders it susceptible to cleavage by the C4b,2a complex. Includes former EC 3.4.21.44. Complement component C2a is in peptidase family S1 (trypsin family)

References: [1232, 1732]

[EC 3.4.21.43 created 1981 (EC 3.4.21.44 created 1981, incorporated 1984)]

[3.4.21.44 Transferred entry. complement component C5 convertase. Now EC 3.4.21.43, classical-complement-pathway C3/C5 convertase]

[EC 3.4.21.44 created 1981, deleted 1984]

EC 3.4.21.45

Accepted name: complement factor I

Reaction: Inactivates complement subcomponents C3b, iC3b and C4b by proteolytic cleavage

Other name(s): complement component C3b inactivator; C3b inactivator; C3b/C4b inactivator; C3bINA; complement C3b/C4b inactivator; complement C4b inactivator; conglutinogen-activating factor C; complement C3b inactivator; factor I; complement C4bi

Comments: Cleavage of complement subcomponent C3b requires its binding to cofactor factor H or complement receptor CR1; cleavage of iC3b requires complement receptor CR1; cleavage of C4b requires C4b-binding protein. In peptidase family S1 (trypsin family)

References: [1752, 457, 1732]

[EC 3.4.21.45 created 1981]

EC 3.4.21.46

Accepted name: complement factor D

Reaction: Selective cleavage of Arg→Lys bond in complement factor B when in complex with complement subcomponent C3b or with cobra venom factor

Other name(s): C3 proactivator convertase; properdin factor D esterase; factor D; factor D (complement)
Comments: A component of the alternative pathway of complement activation. This reaction is analogous to the activation of complement component C2 by complement subcomponent C1s. In peptidase family S1 (trypsin family)

References: [2089, 1732]

[EC 3.4.21.46 created 1981]

EC 3.4.21.47

Accepted name: alternative-complement-pathway C3/C5 convertase

Reaction: Cleavage of Arg→Ser bond in complement component C3 α-chain to yield C3a and C3b, and Arg→bond in complement component C5 α-chain to yield C5a and C5b

Other name(s): complement component C3/C5 convertase (alternative); proenzyme factor B; properdin factor B; C3 proactivator; glycine-rich β-glycoprotein; heat-labile factor; C3 convertase; C3b,Bb,CF,Bb,C5 convertase; (C3b)n,Bb; complement C 3(C 5) convertase (amplification); alternative complement pathway C3(C5) convertase; C5 convertase; CF,Bb; (CVF)-dependent glycine-rich-β-glucoprotein; cobra venom factor-dependent C3 convertase

Comments: A bimolecular complex of complement fragment Bb with either C3b or cobra venom factor; Bb contains the active site. Bb is formed by cleavage of proenzyme factor B by factor D. Cleavage of complement component C5 requires additional C3b which binds C5 and renders it susceptible to cleavage by C3b,Bb complex. C3b,Bb is stabilized in plasma by factor P. Complement factor B is in peptidase family S1 (trypsin family)

References: [1233, 1714, 1732]

[EC 3.4.21.47 created 1981]

EC 3.4.21.48

Accepted name: cerevisin

Reaction: Hydrolysis of proteins with broad specificity, and of Bz-Arg-OEt Ac-Tyr-OEt. Does not hydrolyse peptide amides

Other name(s): yeast proteinase B; proteinase yscB; baker’s yeast proteinase B; brewer’s yeast proteinase; peptidase β

Comments: From Saccharomyces cerevisiae (baker’s yeast, brewer’s yeast). In peptidase family S8 (subtilisin family), but contains a Cys residue near the active site His, and is inhibited by mercurials. Proteinase yscB is a similar enzyme from the yeast Candida albicans [661]

References: [674, 1304, 661, 1688]

[EC 3.4.21.48 created 1972 as EC 3.4.22.9, transferred 1981 to EC 3.4.21.48]

EC 3.4.21.49

Accepted name: hypodermin C

Reaction: Hydrolysis of proteins including native collagen at Ala bond leaving an N-terminal (75%) and a C-terminal (25%) fragment

Other name(s): Hypoderma collagenase

Comments: From the larva of a warble fly, Hypoderma lineatum. Little action on small molecule substrates of trypsin, chymotrypsin, elastase or microbial collagenases. In peptidase family S1 (trypsin family)

References: [1390, 1392, 1391]

[EC 3.4.21.49 created 1981]

EC 3.4.21.50

Accepted name: lysyl endopeptidase

Reaction: Preferential cleavage: Lys→, including -Lys→Pro-

Other name(s): Achromobacter proteinase I (also see Comment); Achromobacter lyticus alkaline proteinase I; protease I; achromopeptidase; lysyl bond specific proteinase
Comments: From Achromobacter lyticus [2612]. Enzymes with similar specificity are produced by Lysobacter en-
yzymogenes (Endoproteinase Lys-C; [1139]) and Pseudomonas aeruginosa (Ps-1; [618]). In peptidase
family S1 (trypsin family)

References: [1584, 1583, 1139, 618, 1872, 2612]

[EC 3.4.21.50 created 1983]

[3.4.21.51 Deleted entry. Leukocyte-membrane neutral endopeptidase]

[EC 3.4.21.51 created 1984, deleted 1992]

[3.4.21.52 Deleted entry. Cathepsin R]

[EC 3.4.21.52 created 1981 as EC 3.4.99.33, transferred 1984 to EC 3.4.21.52, deleted 1992]

EC 3.4.21.53

Accepted name: endopeptidase La

Reaction: Hydrolysis of proteins in presence of ATP

Other name(s): ATP-dependent serine proteinase; lon proteinase; protease La; proteinase La; ATP-dependent lon
proteinase; ATP-dependent protease La; Escherichia coli proteinase La; Escherichia coli serine pro-
teinase La; gene lon protease; gene lon proteins; PIM1 protease; PIM1 proteinase; serine protease La

Comments: Product of the lon gene in Escherichia coli. ATP hydrolysis is linked with peptide bond hydrolysis;
vandate inhibits both reactions. Type example of peptidase family S16. A similar enzyme occurs in
animal mitochondria

References: [523, 1378, 391]

[EC 3.4.21.53 created 1986]

EC 3.4.21.54

Accepted name: γ-renin

Reaction: Cleavage of the Leu—Leu bond in synthetic tetradecapeptide renin substrate (horse), to produce an-
giotensin I, but not active on natural angiotensinogen, unlike renin (EC 3.4.23.15). Also hydrolyses
Bz-Arg-p-nitroanilide

Comments: A member of the tissue kallikrein family, from submandibular glands of male mice. In peptidase fam-
ily S1 (trypsin family)

References: [1993, 582]

[EC 3.4.21.54 created 1986]

EC 3.4.21.55

Accepted name: venombin AB

Reaction: Selective cleavage at Arg— bonds in fibrinogen to form fibrin and release fibrinopeptides A and B

Other name(s): gabonase; okinaxobin II; Bitis gabonica venom serine proteinase; afaâcytin

Comments: From the venom of the Gaboon viper Bitis gabonica. Activates Factor XIII. Not inhibited by an-
tithrombin III/heparin or hirudin, unlike EC 3.4.21.5, thrombin

References: [1984]

[EC 3.4.21.55 created 1989]

[3.4.21.56 Deleted entry. Euphorbain]

[EC 3.4.21.56 created 1972 as EC 3.4.99.7, transferred 1989 to EC 3.4.21.56, deleted 1992]

EC 3.4.21.57

Accepted name: leucyl endopeptidase
Reaction: Hydrolysis of proteins. Preferential cleavage: Leu— in small molecule substrates
Other name(s): plant Leu-proteinase; leucine-specific serine proteinase; leucine endopeptidase; spinach serine protease (leucine specific); spinach leucine-specific serine proteinase; Leu-proteinase
Comments: From leaves of the spinach plant (Spinacia oleracea)
References: [20, 19]

[EC 3.4.21.57 created 1989]

3.4.21.58 Deleted entry. prohormone serine proteinase

[EC 3.4.21.58 created 1989, deleted 1992]

EC 3.4.21.59
Accepted name: tryptase
Reaction: Preferential cleavage: Arg—, Lys—, but with more restricted specificity than trypsin
Other name(s): mast cell tryptase; mast cell protease II; skin tryptase; lung tryptase; pituitary tryptase; mast cell neutral protease; mast cell tryptase; mast cell neutral protease; mast cell serine protease II; mast cell protease II; mast cell serine proteinase tryptase; rat mast cell protease II; tryptase M
Comments: Occurs as a tetrameric molecule with high affinity for heparin, in mast cell granules. In peptidase fam-

ily S1 (trypsin family). Not inhibited by α1-proteinase inhibitor or α2-macroglobulin
References: [2518, 1247, 454, 939, 2680]

[EC 3.4.21.59 created 1992]

EC 3.4.21.60
Accepted name: scutelatin
Reaction: Selective cleavage of Arg—Thr and Arg—Ile in prothrombin to form thrombin and two inactive fragments
Other name(s): taiapan activator; Oxyuranus scutellatus prothrombin-activating proteinase
Comments: From the venom of the Taipan snake (Oxyuranus scutellatus). Converts prothrombin to thrombin in the absence of coagulation Factor Va, and is potentiating by phospholipid and Ca2++. Specificity is sim-
ilar to that of Factor Xa. Binds Ca2+ via γ-carboxyglutamic acid residues. Similar enzymes are known from the venom of other Australian elapid snakes Pseudonaja textilis textilis, Oxyuranus microlepidotus and Demansia muchalis affinis
References: [2720, 2399]

[EC 3.4.21.60 created 1978 as EC 3.4.99.28, transferred 1992 to EC 3.4.21.60]

EC 3.4.21.61
Accepted name: kexin
Reaction: Cleavage of -Lys-Arg— and -Arg-Arg— bonds to process yeast α-factor pheromone and killer toxin precursors
Other name(s): yeast KEX2 protease; proteinase yscF; prohormone-processing exoprotease; paired-basic endopeptidase; yeast cysteine proteinase F (misleading); paired-basic endopeptidase; andrenorphin-Gly-generating enzyme; endoproteinase Kex2p; gene KEX2 dibasic proteinase; Kex 2p proteinase; Kex2 endopeptidase; Kex2 endoprotease; Kex2 endoproteinase; Kex2 protease; proteinase Kex2p; Kex2-like precursor protein processing endoprotease; prohormone-processing KEX2 proteinase; prohormone-processing proteinase; proprotein convertase; protease KEX2; Kex2 proteinase; Kex2-like endoproteinase
Comments: A Ca2+-activated peptidase of peptidase family S8, containing Cys near the active site His, and inhibited by p-mercuribenzoate. Similar enzymes occur in mammals.
References: [1168, 11, 1683, 767, 1684]

[EC 3.4.21.61 created 1989 as EC 3.4.22.23, transferred 1992 to EC 3.4.21.61]
EC 3.4.21.62
Accepted name: subtilisin
Reaction: Hydrolysis of proteins with broad specificity for peptide bonds, and a preference for a large uncharged residue in P1. Hydrolyses peptide amides
Other name(s): alcalase; alcalase 0.6L; alcalase 2.5L; ALK-enzyme; bacillopeptidase A; bacillopeptidase B; *Bacillus subtilis* alkaline proteinase bioprase; bioprase AL 15; bioprase APL 30; colistinase; (see also comments); subtilisin J; subtilisin S41; subtilisin Sendai; subtilisin GX; subtilisin E; subtilisin BL; gene-nase I; esperase; maxatase; alcalase; thermooze PC 10; protease XXVII; thermooze; superase; subtilisin DY; subtilopeptidase; SP 266; savinase 8.0L; savinase 4.0T; kazusase; protease VIII; opticlean; *Bacillus subtilis* alkaline proteinase; protin A 3L; savinase; savinase 16.0L; savinase 32.0 L EX; orientase 10B; protease S
Comments: Subtilisin is a serine endopeptidase, type example of peptidase family S8. It contains no cysteine residues (although these are found in homologous enzymes). Species variants include subtilisin BPN′ (also subtilisin B, subtilopeptidase B, subtilopeptidase C, Nagarse, Nagarse proteinase, subtilisin Novo, bacterial proteinase Novo) and subtilisin Carlsberg (subtilisin A, subtilopeptidase A, alcalase Novo). Similar enzymes are produced by various *Bacillus subtilis* strains and other *Bacillus* species [1920, 1973]


EC 3.4.21.63
Accepted name: oryzin
Reaction: Hydrolysis of proteins with broad specificity, and of Bz-Arg-OEt > Ac-Tyr-OEt. Does not hydrolyse peptide amides
Other name(s): *Aspergillus* alkaline proteinase; aspergillopeptidase B; API 21; aspergillopepsin B; aspergillopepsin F; *Aspergillus candidus* alkaline proteinase; *Aspergillus flavus* alkaline proteinase; *Aspergillus melleus* semi-alkaline proteinase; *Aspergillus oryzae* alkaline proteinase; *Aspergillus parasiticus* alkaline proteinase; *Aspergillus serine proteinase; Aspergillus sydowi* alkaline proteinase; *Aspergillus soya* alkaline proteinase; *Aspergillus melleus* alkaline proteinase; *Aspergillus sulphureus* alkaline proteinase; prozyme; P 5380; kyorinase; seaprose S; semi-alkaline protease; sumizyme MP; prozyme 10; onoprose; onoprose SA; protease P; promelase
Comments: A peptidase of family S8 (subtilisin family), not containing cysteine, that is the predominant extracellular alkaline endopeptidase of the mold *Aspergillus oryzae*. Identical or closely related enzymes are produced by *A. flavus* and *A. sojae* [2,3,4]
References: [1765, 963, 2626, 1705, 2397]


EC 3.4.21.64
Accepted name: peptidase K
Reaction: Hydrolysis of keratin, and of other proteins with subtilisin-like specificity. Hydrolyses peptide amides
Other name(s): *Tritirachium* alkaline proteinase; *Tritirachium album* serine proteinase; proteinase K; *Tritirachium album* proteinase K; endopeptidase K
Comments: From the mold *Tritirachium album* Limber. A peptidase of family S8 (subtilisin family) containing two disulfide bridges and one free Cys near the active site His. Formerly included in EC 3.4.21.14
References: [606, 1708, 1325, 1134, 186]


EC 3.4.21.65
Accepted name: thermomycolin
Reaction: Rather nonspecific hydrolysis of proteins. Preferential cleavage: Ala, Tyr, Phe in small molecule substrates
Other name(s): thermomycolase
Comments: A peptidase of family S8 (subtilisin family) from the thermophilic fungus *Malbranchea pulchella* var. *sulfurea* containing Cys, but not inhibited by p-mercuribenzoate. Very thermostable. Formerly included in EC 3.4.21.14
References: [788]


EC 3.4.21.66
Accepted name: thermitase
Reaction: Hydrolysis of proteins, including collagen
Other name(s): thermophilic *Streptomyces* serine proteinase; *Thermoactinomyces vulgaris* serine proteinase
Comments: A peptidase of family S8 (subtilisin family) from *Thermoactinomyces vulgaris* containing a single Cys, near the active site His, and inhibited by p-mercuribenzoate. The N-terminal extension of the polypeptide chain relative to subtilisin contributes to Ca$^{2+}$-binding and the high thermostability. The amino acid composition and properties of the thermostable enzyme from *Streptomyces rectus* var. *proteolyticus* (formerly included in EC 3.4.21.14) are closely similar [1685, 242]
References: [1685, 242, 1281, 1634, 2539]

[EC 3.4.21.66 created 1992]

EC 3.4.21.67
Accepted name: endopeptidase So
Reaction: Hydrolysis of proteins, but not Bz-Tyr-OEt, Ac-Phe-β-naphthylester, or Bz-Arg-OEt
Other name(s): *E. coli* cytoplasmic proteinase; proteinase So; *Escherichia coli* serine proteinase So
Comments: An *Escherichia coli* cytoplasmic endopeptidase formerly included in EC 3.4.21.14. Inhibited by Tos-Phe-CH$_2$Cl, but not by Tos-Lys-CH$_2$Cl
References: [837, 404]


EC 3.4.21.68
Accepted name: *t*-plasminogen activator
Reaction: Specific cleavage of Arg-Val bond in plasminogen to form plasmin
Other name(s): tissue plasminogen activator; plasminogen activator, tissue-type; tissue-type plasminogen activator; tPA; t-PA
Comments: A peptidase of family S1 (trypsin family) from a wide variety of mammalian tissues, especially endothelial cells. Secreted as a single chain precursor which is cleaved to a two-chain form by plasmin. Activity is considerably enhanced by fibrin. Formerly included in EC 3.4.21.31 and EC 3.4.99.26
References: [1958, 1498, 1962, 2688, 796, 420]

[EC 3.4.21.68 created 1972 as EC 3.4.99.26, transferred 1978 as EC 3.4.21.31, part transferred 1992 to EC 3.4.21.68]

EC 3.4.21.69
Accepted name: protein C (activated)
Reaction: Degradation of blood coagulation factors Va and VIIIa
Other name(s): blood-coagulation factor XIa; activated blood coagulation factor XIV; activated protein C; autoprotrombin II-A; protein Ca; APC; GSAPC

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Comments: A peptidase of family S1 (trypsin family), one of the γ-carboxyglutamic acid-containing coagulation factors. Formed from protein C, the proenzyme that circulates in plasma, by the action of a complex of thrombin with thrombomodulin, or by serine endopeptidases present in several snake venoms

References: [641, 642]

EC 3.4.21.69 created 1992

EC 3.4.21.70

Accepted name: pancreatic endopeptidase E
Reaction: Preferential cleavage: Ala
Other name(s): cholesterol-binding proteinase; proteinase E; cholesterol-binding serine proteinase; pancreatic pro tease E; pancreatic proteinase E; cholesterol-binding pancreatic proteinase; CBPP; pancreas E proteinase
Comments: A peptidase of family S1 (trypsin family) from pancreatic juice. Unlike elastases, has an acidic pI. Binds cholesterol
References: [1549, 2297]

EC 3.4.21.70 created 1992

EC 3.4.21.71

Accepted name: pancreatic elastase II
Reaction: Preferential cleavage: Leu, Met, and Phe. Hydrolyses elastin
Other name(s): pancreatic elastase 2
Comments: A peptidase of family S1 (trypsin family) formed by activation of proelastase II from mammalian pancreas by trypsin. Usually, only one of the pancreatic elastases (see also EC 3.4.21.36) is expressed in a given species; human pancreatic elastase is of type II
References: [702, 2311]

EC 3.4.21.71 created 1992

EC 3.4.21.72

Accepted name: IgA-specific serine endopeptidase
Reaction: Cleavage of immunoglobulin A molecules at certain Pro bonds in the hinge region. No small molecule substrates are known
Other name(s): IgA protease; IgA proteinase; IgA-specific proteinase; immunoglobulin A protease; immunoglobulin A proteinase
Comments: Species variants differing slightly in specificity are secreted by Gram-negative bacteria Neisseria gonorrhoeae and Haemophilus influenzae. Type example of peptidase family S6. Some other bacterial endopeptidases with similar specificity are of metallo-type (see EC 3.4.24.13, IgA-specific metalloendopeptidase)
References: [1988, 101]

EC 3.4.21.72 created 1992

EC 3.4.21.73

Accepted name: u-plasminogen activator
Reaction: Specific cleavage of Arg–Val bond in plasminogen to form plasmin
Other name(s): urokinase; urinary plasminogen activator; cellular plasminogen activator; urokinase-type plasminogen activator; double-chain urokinase-type plasminogen activator; two-chain urokinase-type plasminogen activator; urokinase plasminogen activator; uPA; u-PA; abbokinase; urinary esterase A
Comments: Formed from the inactive precursor by action of plasmin or plasma kallikrein. Differs in structure from t-plasminogen activator (EC 3.4.21.68), and does not bind to fibrin. In peptidase family S1 (trypsin family). Formerly included in EC 3.4.21.31 and EC 3.4.99.26
References: [1500, 1498, 2189, 420, 1458]
EC 3.4.21.74
Accepted name: venombin A
Reaction: Selective cleavage of Arg bond in fibrinogen, to form fibrin, and release fibrinopeptide A. The specificity of further degradation of fibrinogen varies with species origin of the enzyme
Other name(s): α-fibrinogenase; habutobin; zinc metalloproteinase Cbfib1.1; zinc metalloproteinase Cbfib1.2; zinc metalloproteinase Cbfib2; ancrod; (see also Comments)
Comments: A somewhat thrombin-like enzyme from venoms of snakes of the viper/rattlesnake group. Species variants of the enzyme include ancrod from Agkistrodon rhodostoma (Malayan pit viper) (formerly EC 3.4.21.28) [1824], batroxobin from Bothrops atrox (South American pit viper) (formerly EC 3.4.21.29) [2430, 1104] and crotalase from Crotalus adamanteus (Eastern diamondback rattlesnake) (formerly EC 3.4.21.30) [1566, 2332]. In peptidase family S1 (trypsin family). Does not require activation by Ca²⁺
References: [1824, 2430, 1566, 2332, 1104]

EC 3.4.21.75
Accepted name: furin
Reaction: Release of mature proteins from their proproteins by cleavage of -Arg-Xaa-Yaa-Arg bonds, where Xaa can by any amino acid and Yaa is Arg or Lys. Releases albumin, complement component C3 and von Willebrand factor from their respective precursors
Other name(s): prohormone convertase; dibasic processing enzyme; PACE; paired basic amino acid cleaving enzyme; paired basic amino acid converting enzyme; serine proteinase PACE; PC1; SPC3; proprotein convertase
Comments: One of a group of peptidases in peptidase family S8 (subtilisin family) that is structurally and functionally similar to kexin. All are activated by Ca²⁺, contain Cys near the active site His, and are inhibited by p-mercuribenzoate. At least three related enzymes are recognized in mammals: PC2, PC3 and PC4, which have somewhat different specificities
References: [504, 503, 953, 2271, 2418]

EC 3.4.21.76
Accepted name: myeloblastin
Reaction: Hydrolysis of proteins, including elastin, by preferential cleavage: -Ala-Val-
Other name(s): leukocyte proteinase 3; leukocyte proteinase 4; Wegener’s granulomatosis autoantigen;proteinase PR-3; proteinase-3; PMNL proteinase
Comments: From polymorphonuclear leukocyte granules. In peptidase family S1 (trypsin family). Not inhibited by secretory leukocyte proteinase inhibitor
References: [1371, 2060, 291, 1184]

EC 3.4.21.77
Accepted name: semenogelase
Reaction: Preferential cleavage: -Tyr-
Other name(s): prostate-specific antigen; α-semionoprotein; seminin; P-30 antigen; antigen (human clone HPSA-1 prostate-specific protein moiety reduced); γ-semionglycoprotein (human protein moiety reduced); γ-SM; antigen PSA (human prostate-specific); human glandular kallikrein; antigen PSA (human clone SP1 protein moiety reduced)
Comments: A peptidase of family S1 (trypsin family) from seminal plasma. Slowly inhibited by α₁-antichymotrypsin
References: [544, 401]

[EC 3.4.21.77 created 1993]

EC 3.4.21.78

Accepted name: granzyme A

Reaction: Hydrolysis of proteins, including fibronectin, type IV collagen and nucleolin. Preferential cleavage: -Arg-> -Phe in small molecule substrates

Other name(s): CTLA3; HuTPS; T-cell associated protease 1; cytotoxic T lymphocyte serine protease; TSP-1; T-cell derived serine proteinase

Comments: From cytotoxic T lymphocyte granules. In peptidase family S1 (trypsin family). The human enzyme does not cleave Phe-

References: [2334, 799, 1857]

[EC 3.4.21.78 created 1993]

EC 3.4.21.79

Accepted name: granzyme B

Reaction: Preferential cleavage: -Asp-> -Asn-> -Met, -Ser

Other name(s): CTLA1; CCPII; cytotoxic cell proteinase-1; granzyme G; granzyme H; CCP1 proteinase

Comments: From cytotoxic T lymphocyte granules. In peptidase family S1 (trypsin family)

References: [2245, 1857, 1992]

[EC 3.4.21.79 created 1993]

EC 3.4.21.80

Accepted name: streptogrisin A

Reaction: Hydrolysis of proteins with specificity similar to chymotrypsin

Other name(s): Streptomyces griseus protease A; protease A; proteinase A; Streptomyces griseus proteinase A; Streptomyces griseus serine proteinase 3; Streptomyces griseus serine proteinase A

Comments: From Streptomyces griseus. A component of Pronase, in family S1 (trypsin family). Not inhibited by Tos-Phe-CH2Cl or ovomucoid

References: [1152, 2323, 1131, 515, 979]

[EC 3.4.21.80 created 1993]

EC 3.4.21.81

Accepted name: streptogrisin B

Reaction: Hydrolysis of proteins with trypsin-like specificity

Other name(s): Streptomyces griseus protease B; pronase B; serine proteinase B; Streptomyces griseus proteinase B; Streptomyces griseus serine proteinase B

Comments: From Streptomyces griseus. A component of Pronase, in peptidase family S1 (trypsin family), distinct from Streptomyces trypsin

References: [1171, 754, 2077, 979, 867]

[EC 3.4.21.81 created 1993]

EC 3.4.21.82

Accepted name: glutamyl endopeptidase II

Reaction: Preferential cleavage: -Glu-> -Asp. Preference for Pro or Leu at P2 and Phe at P3. Cleavage of -Glu-Asp- and -Glu-Pro- bonds is slow

Other name(s): GluSGP

References: [544, 401]
Comments: From *Streptomyces griseus*. A peptidase of family S1 (trypsin family). Inhibited by [Leu$^{18}$$\rightarrow$Glu]-modified turkey ovomucoid third domain

References: [2893, 1305, 1754, 2466, 262]

[EC 3.4.21.82 created 1993]

EC 3.4.21.83
Accepted name: oligopeptidase B
Reaction: Hydrolysis of -Arg, -Lys bonds in oligopeptides, even when P1' residue is proline
Other name(s): protease II, *Escherichia coli* alkaline proteinase II; protease II
Comments: Known from *Escherichia coli*. Inhibited by Tos-Lys-CH$_2$Cl. In peptidase family S9 (prolyl oligopeptidase family)

References: [1192]

[EC 3.4.21.83 created 1993]

EC 3.4.21.84
Accepted name: limulus clotting factor C
Reaction: Selective cleavage of -Arg$^{103}$Ser- and -Ile$^{124}$Ile- bonds in limulus clotting factor B to form factor B. Cleavage of -Pro-Arg bonds in synthetic substrates
Other name(s): factor C; limulus factor C
Comments: From the hemocyte granules of the horseshoe crabs *Limulus* and *Tachypleus*. Factor C is activated by Gram-negative bacterial lipopolysaccharides and chymotrypsin. Inhibited by antithrombin III. In peptidase family S1 (trypsin family)

References: [1776, 1742, 2571]

[EC 3.4.21.84 created 1993]

EC 3.4.21.85
Accepted name: limulus clotting factor B
Reaction: Selective cleavage of -Arg$^{98}$Ile- bond in limulus proclotting enzyme to form active clotting enzyme
Comments: From the hemocyte granules of the horseshoe crabs *Limulus* and *Tachypleus*. Factor B is activated by limulus clotting factor C. In peptidase family S1 (trypsin family)

References: [1775]

[EC 3.4.21.85 created 1993]

EC 3.4.21.86
Accepted name: limulus clotting enzyme
Reaction: Selective cleavage of -Arg$^{18}$ and -Arg$^{47}$ bonds in coagulogen to form coagulin and fragments
Other name(s): clotting enzyme
Comments: From the hemocyte granules of horseshoe crabs *Limulus* and *Tachypleus*. Proclotting enzyme is activated by limulus clotting factor . In peptidase family S1 (trypsin family)

References: [1741, 2571]

[EC 3.4.21.86 created 1993]

[3.4.21.87 Transferred entry. omptin. Now EC 3.4.23.49, omptin. The enzyme is not a serine protease, as thought previously, but an aspartate protease]

[EC 3.4.21.87 created 1993, deleted 2006]

EC 3.4.21.88
<table>
<thead>
<tr>
<th>Accepted name:</th>
<th>repressor LexA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reaction:</td>
<td>Hydrolysis of Ala$^{84}$→Gly bond in repressor LexA</td>
</tr>
<tr>
<td>Other name(s):</td>
<td>LexA repressor</td>
</tr>
<tr>
<td>Comments:</td>
<td>RecA protein and single-stranded DNA are required for activity, which is attributed to a Ser/Lys dyad [2360]. The LexA protein represses the SOS regulon, which regulates the genes involved in DNA repair. In the presence of single-stranded DNA, the RecA protein interacts with repressor LexA, causing it to undergo an autocatalytic cleavage which disrupts the DNA-binding part of the repressor, and inactivates it. The consequent derepression of the SOS regulon leads to DNA repair. This peptidase activity of LexA was previously attributed to the RecA protein. Type example of peptidase family S24</td>
</tr>
<tr>
<td>References:</td>
<td>[1041, 2360, 1253, 1481]</td>
</tr>
</tbody>
</table>

**EC 3.4.21.89**

<table>
<thead>
<tr>
<th>Accepted name:</th>
<th>signal peptidase I</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reaction:</td>
<td>Cleavage of hydrophobic, N-terminal signal or leader sequences</td>
</tr>
<tr>
<td>Other name(s):</td>
<td>leader peptidase I; signal proteinase; <em>Escherichia coli</em> leader peptidase; eukaryotic signal peptidase; eukaryotic signal proteinase; leader peptidase; leader peptide hydrolase; leader proteinase; signal peptidase; pilin leader peptidase; SPC; prokaryotic signal peptidase; prokaryotic leader peptidase; HOSP; prokaryotic signal proteinase; propeptidase; PuIO prepeptide; signal peptidase; signalase; bacterial leader peptidase I; pilin leader peptidase</td>
</tr>
<tr>
<td>Comments:</td>
<td>The enzyme is found in bacterial membranes and in chloroplast thylakoid membranes. Unaffected by inhibitors of most serine peptidases, but site-directed mutagenesis implicates a Ser/Lys catalytic dyad in activity [205, 2603]. Hydrolyses a single bond-Ala→Ala- in M13 phage procoat protein, producing free signal peptide and coat protein. Formerly included in EC 3.4.99.36. Eukaryote signal peptidases that may have somewhat different specificity are known from the endoplasmic reticulum membrane [1487] and mitochondrial inner membrane [1838]. Type example of peptidase family S26</td>
</tr>
<tr>
<td>References:</td>
<td>[205, 1838, 2603, 1487, 2602, 353, 1094]</td>
</tr>
</tbody>
</table>

**EC 3.4.21.90**

<table>
<thead>
<tr>
<th>Accepted name:</th>
<th>togavirin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reaction:</td>
<td>Autocatalytic release of the core protein from the N-terminus of the togavirus structural polyprotein by hydrolysis of a -Trp→Ser- bond</td>
</tr>
<tr>
<td>Other name(s):</td>
<td>Sindbis virus protease; Sindbis virus core protein; NsP2 proteinase</td>
</tr>
<tr>
<td>Comments:</td>
<td>Known from the Sindbis and Semliki forest togaviruses. Once released, the core protein does not retain catalytic activity. Togavirin is the type example of peptidase family S3 and has a similar tertiary structure to chymotrypsin [2580]</td>
</tr>
<tr>
<td>References:</td>
<td>[1326, 2434, 2580]</td>
</tr>
</tbody>
</table>

**EC 3.4.21.91**

<table>
<thead>
<tr>
<th>Accepted name:</th>
<th>flavivirin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reaction:</td>
<td>Selective hydrolysis of -Xaa-Xaa→Yaa- bonds in which each of the Xaa can be either Arg or Lys and Yaa can be either Ser or Ala</td>
</tr>
<tr>
<td>Other name(s):</td>
<td>Yellow fever virus (flavivirus) protease; NS2B-3 proteinase</td>
</tr>
<tr>
<td>Comments:</td>
<td>Known from classical flaviviruses (yellow fever, dengue fever). The functional viral peptidase is part of the NS2B protein. Catalytic His, Asp and Ser residues are arranged as in chymotrypsin, but flavivirin is the type example of peptidase family S7</td>
</tr>
<tr>
<td>References:</td>
<td>[354, 323, 1462]</td>
</tr>
</tbody>
</table>
EC 3.4.21.92
Accepted name: endopeptidase Clp
Reaction: Hydrolysis of proteins to small peptides in the presence of ATP and Mg\(^{2+}\). α-Casein is the usual test substrate. In the absence of ATP, only oligopeptides shorter than five residues are hydrolysed (such as succinyl-Leu-Tyr-NHMe; and Leu-Tyr-Leu-Tyr-Trp, in which cleavage of the -Tyr-Leu- and -Tyr-Trp bonds also occurs)

Other name(s): endopeptidase Ti; caseinolytic protease; protease Ti; ATP-dependent Clp protease; endopeptidase Ti; caseinolytic protease; ClpP; Clp protease

Comments: An enzyme from bacteria that contains subunits of two types, ClpP, with peptidase activity, and ClpA, with ATPase activity. The ClpAP complex, which displays ATP-dependent endopeptidase activity, has the composition (ClpP\(_{14}\)ClpA\(_{6}\))\(_2\) [1237]. ClpP is the type example of peptidase family S14

References: [853, 1602, 1603, 1237]

EC 3.4.21.93
Accepted name: proprotein convertase 1
Reaction: Release of protein hormones, neuropeptides and renin from their precursors, generally by hydrolysis of -Lys-Arg- bonds

Other name(s): prohormone convertase 3; neuroendocrine convertase 1; PC1

Comments: A Ca\(^{2+}\)-dependent enzyme, maximally active at about pH 5.5. Substrates include pro-opiomelanocortin, prorenin, proenkephalin, prodynorphin, prosomatostatin and proinsulin. Unlike prohormone convertase 2, does not hydrolyse proluteinizing-hormone-releasing-hormone. Unusually, processing of prodynorphin occurs at a bond in which P2 is Thr. Present in the regulated secretory pathway of neuroendocrine cells, commonly acting co-operatively with prohormone convertase 2. In peptidase family S8 (subtilisin family)

References: [2274, 2363, 2418, 2272, 1136]

EC 3.4.21.94
Accepted name: proprotein convertase 2
Reaction: Release of protein hormones and neuropeptides from their precursors, generally by hydrolysis of -Lys-Arg- bonds

Other name(s): neuroendocrine convertase 2; PC2

Comments: A Ca\(^{2+}\)-dependent enzyme, maximally active at about pH 5.5. Specificity is broader than that of prohormone convertase 1. Substrates include pro-opiomelanocortin, proenkephalin, prodynorphin, proglucagon, proinsulin and proluteinizing-hormone-releasing-hormone. Does not hydrolyse prorenin or prosomatostatin, however. Unusually, processing of prodynorphin occurs at a bond in which P2 is Thr. Present in the regulated secretory pathway of neuroendocrine cells, commonly acting co-operatively with prohormone convertase 1. In peptidase family S8 (subtilisin family)

References: [2274, 2364, 2152, 2272]

EC 3.4.21.95
Accepted name: snake venom factor V activator
Reaction: Fully activates human clotting factor V by a single cleavage at the Trp-Tyr-Leu-Arg\(^{1545}\)Ser-Asn-Asn-Gly bond. Cattle, but not rabbit, factor V is cleaved, and no other proteins of the clotting system are attacked. Esterase activity is observed on Bz-Arg-OEt and Tos-Arg-OMe, and amidase activity on Phe-pipoccolyl-Arg-NHPhNO\(_2\)

References: [595, 853]
Comments: Known from venom of Vipera russelli. Inhibited by di-isopropyl fluorophosphate, unlike the metalloprotease russellysin (EC 3.4.24.58) that is specific for factor X [1275]. In peptidase family S1 (trypsin family) [2570].

References: [1275, 2570]

[EC 3.4.21.95 created 1997]

EC 3.4.21.96
Accepted name: lactocepin
Reaction: Endopeptidase activity with very broad specificity, although some subsite preferences have been noted, e.g. large hydrophobic residues in the P1 and P4 positions, and Pro in the P2 position [1,2]. Best known for its action on caseins, although it has been shown to hydrolyse hemoglobin and oxidized insulin B chain
Other name(s): CEP; extracellular lactococcal proteinase; lactococcal cell wall-associated proteinase; lactococcal cell envelope-associated proteinase; PrtP
Comments: Associated with the cell envelope of Lactococcus lactis and attached via a C-terminal membrane anchor sequence. Responsible for the hydrolysis of casein in milk and the provision of peptides essential to cell growth. Important in cheese making and the production of lactic casein, being required for rapid growth to high cell densities with concomitant production of adequate levels of lactic acid. Specificity differences between lactocepins from different starter strains may be partly responsible for imparting different flavour qualities to cheese [2020]. In peptidase family S8 (subtilisin family)
References: [2696, 1694, 651, 2020]

[EC 3.4.21.96 created 1997]

EC 3.4.21.97
Accepted name: assemblin
Reaction: Cleaves -Ala-Ser- and -Ala-Ala- bonds in the scaffold protein
Comments: Inolved in the breakdown of the scaffold protein during the late stages of assembly of the herpesvirus virion. Inhibited by diisopropyl fluorophosphate. Type example of peptidase family S21. Catalytic residues are His, Ser, His, a combination not known for any other peptidase, and the protein fold also is unique. Known from herpes viruses of several types, cytomegalovirus, Epstein-Barr virus and human herpesvirus 3
References: [376, 478]

[EC 3.4.21.97 created 2000]

EC 3.4.21.98
Accepted name: hepacivirin
Reaction: Hydrolysis of four peptide bonds in the viral precursor polyprotein, commonly with Asp or Glu in the P6 position, Cys or Thr in P1 and Ser or Ala in P1
Other name(s): Cpro-2; hepatitis C virus NS3 serine proteinase; NS3-4A serine proteinase complex
Comments: Encoded by the genome of the viruses of the hepatitis C group, and contributes to the maturation of the precursor polyproteins. The enzyme is greatly activated by binding of the 54-residue NS4A ‘co-factor’ protein also derived from the viral polyprotein. Type example of peptidase family S29. The crystallographic structure shows a chymotrypsin-like fold
References: [1260, 2106]

[EC 3.4.21.98 created 2000]

EC 3.4.21.99
Accepted name: spermosin
Reaction: Hydrolyses arginyl bonds, preferably with Pro in the P2 position

References: [165]
The enzyme from the ascidian (Prochordate) *Halocynthia roretzi* is localized in the sperm head, and released during sperm activation. A proline-rich region is involved in binding to the vitelline coat of the egg. Belongs in peptidase family S1 (trypsin family).

References: [2217, 2218, 2215, 2216]

[EC 3.4.21.99 created 2001]

**EC 3.4.21.100**

**Accepted name:** sedolisin

**Reaction:** Hydrolysis of the B chain of insulin at -Glu$^{13}$→Ala-, -Leu$^{15}$→Tyr- and -Phe$^{25}$→Tyr-, and angiotensin I at -Tyr$^{4}$→Ile-. A good synthetic substrate is Lys-Pro-Ile-Glu-Phe-Phe(NO$_2$)-Arg-Leu.

**Other name(s):** *Pseudomonas* sp. pepstatin-insensitive carboxyl proteinase; pseudomonapepsin; pseudomonalisin; sedolysin

**Comments:** An enzyme secreted by *Pseudomonas* sp. No. 101. Optimum pH is 4. It is distinguished from xanthomonapepsin by its insensitivity to EPNP and from scytalidopepsin B by this property and by its unrelated amino-acid sequence. Inhibited by tyrostatin, a peptide aldehyde [1852]. Type example of peptidase family S53.

References: [1854, 1852, 2816, 2817]

[EC 3.4.21.100 created 1995 as EC 3.4.23.37, transferred 2001 to EC 3.4.21.100, modified 2003]

**EC 3.4.21.101**

**Accepted name:** xanthomonalisin

**Reaction:** Cleavage of casein

**Other name(s):** *Xanthomonas* aspartic proteinase; xanthomonapepsin; sedolisin-B

**Comments:** Secreted by the bacterium *Xanthomonas* sp. Belongs in peptidase family S53.

References: [1853, 2817]

[EC 3.4.21.101 created 1995 as EC 3.4.23.33, transferred 2001 to EC 3.4.21.101, modified 2003]

**EC 3.4.21.102**

**Accepted name:** C-terminal processing peptidase

**Reaction:** The enzyme shows specific recognition of a C-terminal tripeptide, Xaa-Yaa-Zaa, in which Xaa is preferably Ala or Leu, Yaa is preferably Ala or Tyr, and Zaa is preferably Ala, but then cleaves at a variable distance from the C-terminus. A typical cleavage is -Ala-Ala→Arg-Ala-Ala-Lys-Glu-Asn-Tyr-Ala-Leu-Ala-Ala. In the plant chloroplast, the enzyme removes the C-terminal extension of the D1 polypeptide of photosystem II

**Other name(s):** CtpA gene product (*Synechocystis* sp.); photosystem II D1 protein processing peptidase; protease Re; tail-specific protease; Tsp protease

**Comments:** Proteolytic processing of the D1 protein of photosystem II is necessary to allow the light-driven assembly of the tetracahedral manganese cluster, which is responsible for photosynthetic water oxidation. The recognition of the substrate is mediated by a PDZ domain, a small protein module that promotes protein-protein interactions by binding to internal or C-terminal sequences of their partner proteins. Type example of peptidase family S41.

References: [1223, 165, 1451]

[EC 3.4.21.102 created 2001]

**EC 3.4.21.103**

**Accepted name:** physarolisin

**Reaction:** Milk clotting activity. Preferential cleavage of Gly$^{8}$→Ser in B chain of insulin most rapidly, followed by Leu$^{11}$→Val, Cys(SO$_3$H)$^{19}$→Gly and Phe$^{24}$→Phe. No action on Ac-Phe-Tyr(I)$_2$.

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Other name(s): Dictyostelium discoideum aspartic proteinase; Dictyostelium discoideum aspartic proteinase E; Physarum flavicomum aspartic proteinase; Physarum polycephalum acid proteinase; Physarum aspartic proteinase; physaropepsin

Comments: Belongs in peptidase family S53. From the slime mold Physarum polycephalum. Is not inhibited by pepstatin, but is blocked by methyl 2-diazaacetamidohexanoate. Closely similar enzymes are found in Dictyostelium discoideum and P. flavicomum. Formerly included in EC 3.4.23.6.

References: [983, 1735, 1832, 2817, 1814]

[EC 3.4.21.103 created 1992 as EC 3.4.23.27, EC 3.4.23.6 created 1992, EC 3.4.23.6 created 1961 as EC 3.4.4.17, transferred 1972 to EC 3.4.23.6, modified 1981, EC 3.4.23.7, EC 3.4.23.8, EC 3.4.23.9, EC 3.4.23.10, EC 3.4.99.1, EC 3.4.99.15 and EC 3.4.99.25 all created 1972 and incorporated 1978, part incorporated 1992, transferred 2003 to EC 3.4.21.103]
EC 3.4.21.107

Accepted name: peptidase Do

Reaction: Acts on substrates that are at least partially unfolded. The cleavage site P1 residue is normally between a pair of hydrophobic residues, such as Val–Val

Other name(s): DegP; DegP protease; HtrA; high temperature requirement protease A; HrtA heat shock protein; protease Do; Do protease

Comments: This serine endopeptidase is essential for the clearance of denatured or aggregated proteins from the inner-membrane and periplasmic space in Escherichia coli. Natural substrates of the enzyme include colicin A lysis protein, pilin subunits and MalS from E. coli [1156]. The enzyme has weak peptidase activity with casein and other non-native substrates [1156]. The peptidase acts as a chaperone at low temperatures but switches to a peptidase (heat shock protein) at higher temperatures [1477, 1332]. Molecular chaperones and peptidases control the folded state of proteins by recognizing hydrophobic stretches of polypeptide that become exposed by misfolding or unfolding. They then bind these hydrophobic substrates to prevent aggregation or assist in protein refolding. If attempts at refolding fail, then irreversibly damaged proteins are degraded by peptidases such as this enzyme [1332]. Belongs in peptidase family S1C.

References: [1477, 2278, 1156, 2467, 1931, 1332]

EC 3.4.21.108

Accepted name: HtrA2 peptidase

Reaction: Cleavage of non-polar aliphatic amino-acids at the P1 position, with a preference for Val, Ile and Met. At the P2 and P3 positions, Arg is selected most strongly with a secondary preference for other hydrophilic residues

Other name(s): high temperature requirement protein A2; HtrA2; Omi stress-regulated endoprotease; serine proteinase OMI; HtrA2 protease; OMI/HtrA2 protease; HtrA2/Omi; Omi/HtrA2

Comments: This enzyme is upregulated in mammalian cells in response to stress induced by both heat shock and tunicamycin treatment [859]. It can induce apoptosis in a caspase-independent manner through its peptidase activity and in a caspase-dependent manner by disrupting the interaction between caspase and the inhibitor of apoptosis (IAP) [1579]. Belongs in peptidase family S1C.

References: [2405, 2214, 1579, 859, 1445]

EC 3.4.21.109

Accepted name: matriptase

Reaction: Cleaves various synthetic substrates with Arg or Lys at the P1 position and prefers small side-chain amino acids, such as Ala and Gly, at the P2 position

Other name(s): serine protease 14; membrane-type serine protease 1; MT-SP1; prostatin; serine protease TADG-15; tumor-associated differentially-expressed gene 15 protein; ST14; breast cancer 80 kDa protease; epithin; serine endopeptidase SNC19

Comments: This trypsin-like integral-membrane serine peptidase has been implicated in breast cancer invasion and metastasis [1407, 1463]. The enzyme can activate hepatocyte growth factor/scattering factor (HGF/SF) by cleavage of the two-chain form at an Arg residue to give active α- and β-HGF, but it does not activate plasminogen, which shares high homology with HGF [1407]. The enzyme can also activate urokinase plasminogen activator (uPA), which initiates the matrix-degrading peptidase cascade [1407, 1463]. Belongs in peptidase family S1A.

References: [1407, 1463]
EC 3.4.21.110
Accepted name: C5a peptidase
Reaction: The primary cleavage site is at His$^{67}$-Lys$^{68}$ in human C5a with a minor secondary cleavage site at Ala$^{58}$-Ser$^{59}$
Other name(s): streptococcal C5a peptidase; ScpA; ScpB; SCPA
Comments: This enzyme is a surface-associated subtilisin-like serine peptidase with very specific substrate specificity. Virulent strains of streptococci, including Streptococcus pyogenes, can evade human detection and phagocytosis by destroying the complement chemotaxin C5a. Cleavage of human C5a by this enzyme reduces the ability of C5a to bind receptors on the surface of polymorphonuclear neutrophil leukocytes (PMNLs) and thereby abolishes its chemotactic properties [2783, 49]. Belongs in peptidase family S8A.
References: [2783, 231, 414, 49, 2412, 2541]

[EC 3.4.21.110 created 2006]

EC 3.4.21.111
Accepted name: aqualysin 1
Reaction: Exhibits low specificity towards esters of amino acids with small hydrophobic or aromatic residues at the P1 position
Other name(s): caldolysin
Comments: This enzyme from the extreme thermophile, Thermus aquaticus, is an alkaline serine peptidase. It has three subsites, S1, S2, and S3, in the substrate binding site. The preferred amino acids at the S1 site are Ala and Phe, at the S2 site are Ala and norleucine and at the S3 site are Phe and Ile [2517]. These specificities are similar to those of EC 3.4.21.64 (peptidase K) and EC 3.4.21.62 (subtilisin BPN′) [2517]. The enzyme displays broad specificity for cleavage of insulin B-chain and hydrolyses elastin substrates such as succinyl-(Ala)$_n$-p-nitroanilide ($n = 1, 2, 3$) and some peptide esters [1596, 2517]. Belongs in peptidase family S8A.
References: [1596, 2516, 2517]

[EC 3.4.21.111 created 2006]

EC 3.4.21.112
Accepted name: site-1 protease
Reaction: Processes precursors containing basic and hydrophobic/aliphatic residues at P4 and P2, respectively, with a relatively relaxed acceptance of amino acids at P1 and P3
Other name(s): mammalian subtilisin/kexin isozyme 1; membrane-bound transcription factor site-1 protease; proprotein convertase SKI-1; proprotein convertase SKI-1/S1PPS1; S1P endopeptidase; S1P protease; site-1 peptidase; site-1 protease; SKI-1; SREBP protease; SREBP S1 protease; SREBP-2 protease; sterol regulatory element-binding protein protease; sterol regulatory element-binding protein site 1 protease; sterol-regulated luminal protease; subtilase SKI-1/S1P; subtilisin/kexin-isozyme 1
Comments: Cleaves sterol regulatory element-binding proteins (SREBPs) and thereby initiates a process by which the active fragments of the SREBPs translocate to the nucleus and activate genes controlling the synthesis and uptake of cholesterol and unsaturated fatty acids into the bloodstream [643]. The enzyme also processes pro-brain-derived neurotrophic factor and undergoes autocatalytic activation in the endoplasmic reticulum through sequential cleavages [1422]. The enzyme can also process the unfolded protein response stress factor ATF6 at an Arg-His-Lys-Lys$^-$ site [2879, 2273], and the envelope glycoprotein of the highly infectious Lassa virus [1422, 2273] and Crimean Congo hemorrhagic fever virus at Arg-Arg-Lys-Lys$^-$ [2695, 2273]. Belongs in peptidase family S8A.
References: [643, 382, 2586, 2879, 1422, 148, 2695, 2273]

[EC 3.4.21.112 created 2006]

EC 3.4.21.113

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Accepted name: pestivirus NS3 polyprotein peptidase
Reaction: Leu is conserved at position P1 for all four cleavage sites. Alanine is found at position P1′ of the NS4A-NS4B cleavage site, whereas serine is found at position P1′ of the NS3-NS4A, NS4B-NS5A and NS5A-NS5B cleavage sites
Other name(s): border disease virus NS3 endopeptidase; BDV NS3 endopeptidase; bovine viral diarrhea virus NS3 endopeptidase; BVDV NS3 endopeptidase; classical swine fever virus NS3 endopeptidase; CSFV NS3 endopeptidase; p80
Comments: The polyprotein of noncytopathogenic pestiviruses is cleaved co- and post-translationally into at least 11 proteins (Npro, C, Ecrns, E1, E2, p7, NS2-3, NS4A, NS4B, NS5A, and NS5B) [2533]. The genomes of cytopathogenic pestivirus strains express at least one additional protein, called NS3 (p80) [2533]. This enzyme, which resides in the N-terminal region of NS3 (nonstructural protein 3), is essential for generation of its own C-terminus and for processing of the downstream cleavage sites, leading to the release of the pestivirus nonstructural proteins NS4A, NS4B, NS5A and NS5B [2813, 2533]. Belongs in peptidase family S31.
References: [2813, 2533, 2837, 2534]

[EC 3.4.21.113 created 2006]

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EC 3.4.21.114
Accepted name: equine arterivirus serine peptidase
Reaction: Cleavage of (Glu/Gln)–(Gly/Ser/Ala) in arterivirus replicase translation products ORF1a and ORF1ab
Comments: In the equine arterivirus (EAV), the replicase gene is translated into open reading frame 1a (ORF1a) and ORF1ab polyproteins. This enzyme is the main viral proteinase and processes five cleavage sites in the ORF1a protein and three in the ORF1b-encoded part of the ORF1ab protein to yield nonstructural proteins (nsp5-nsp12) [144]. It combines the catalytic system of a chymotrypsin-like serine peptidase (His-Asp-Ser catalytic triad) with the substrate specificity of a 3C-like serine peptidase (Glu or Gln) at the P1 position and a small amino-acid residue (Gly, Ser or Ala) at the P1′ position [2373]. Cleavage of ORF1ab by this enzyme is essential for viral replication [2675]. Belongs in peptidase family S32.
References: [2373, 2675, 144]

[EC 3.4.21.114 created 2006]

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EC 3.4.21.115
Accepted name: infectious pancreatic necrosis birnavirus Vp4 peptidase
Reaction: Cleaves the (Ser/Thr)-Xaa-Ala–(Ser/Ala)-Gly motif in the polyprotein NH2-pVP2-VP4-VP3-COOH of infectious pancreatic necrosis virus at the pVP2-VP4 and VP4-VP3 junctions
Other name(s): infectious pancreatic necrosis virus protease; IPNV Vp4 protease; IPNV Vp4 peptidase; NS protease; NS-associated protease; Vp4 protease
Comments: Infectious pancreatic necrosis virus (IPNV) is a birnavirus that causes an acute, contagious disease in young salmonid fish [1963]. As with most viruses that infect eukaryotic cells, the proteolytic processing of viral precursor proteins is a crucial step in the life cycle of this virus [1963]. pVP2 is converted into VP2 by cleavage near the carboxy end of pVP2. This cleavage is most likely due to host-cell proteases rather than VP4 [1963, 553]. Differs from most serine peptidases in not having the catalytic triad Ser-His-Asp [1963]. Belongs in peptidase family S50.
References: [1557, 1963, 553]

[EC 3.4.21.115 created 2006]

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EC 3.4.21.116
Accepted name: SpoIVB peptidase
Reaction: Self-cleaves Val52–Asn53, Ala62–Phe63 and Val74–Thr75 at the N-terminus of SpoIVB
Other name(s): sporulation factor IV B protease
Comments: This enzyme plays a central role in a regulatory checkpoint (the σ^K checkpoint), which coordinates gene expression during the later stages of spore formation in *Bacillus subtilis* [2719, 1020]. The enzyme activates proteolytic processing of a sporulation-specific sigma factor, pro-σ^K, to its mature and active form, σ^K, by self-cleavage [2719, 1020]. The enzyme is also subject to secondary proteolysis, which presumably inactivates SpoIVB [1020]. The enzyme is also essential for the formation of heat-resistant spores. Belongs in peptidase family S55.

References: [2719, 1019, 1020, 565]

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**EC 3.4.21.117**

Accepted name: stratum corneum chymotryptic enzyme

Reaction: Cleavage of proteins with aromatic side chains in the P1 position

Other name(s): kallikrein 7; SCCE; KLK7; PRSS6; hK7

Comments: This enzyme has wide substrate specificity, being able to degrade heat-denatured bovine casein and the α-chain of native human fibrinogen. It cleaves the B chain of bovine insulin at Leu^{6}→Cya^{7}, Tyr^{16}→Leu^{17}, Phe^{25}→Tyr^{26} and Tyr^{26}→Thr^{27} [2357]. It is thought to play a role in the desquamation (skin-shedding) of the outer layer of skin, the stratum corneum, by degrading intercellular cohesive structures [2357, 609]. Belongs in peptidase family S1A.

References: [2357, 609, 922, 2898, 2684]

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**EC 3.4.21.118**

Accepted name: kallikrein 8

Reaction: Cleavage of amide substrates following the basic amino acids Arg or Lys at the P1 position, with a preference for Arg over Lys

Other name(s): KLK8; PRSS19; human kallikrein 8; hK8; mK8; ovasin; tumor-associated differentially expressed gene 14; TADG-14; NP; neuropsin

Comments: The enzyme is activated by removal of an N-terminal prepropeptide [2303, 1273]. The highest amidolytic activity is observed using Boc-Val-Pro-Arg→7-amido-4-methylcoumarin, which is a substrate of α-thrombin [2303, 1273]. Substrates lacking basic amino acids in the P1 position are not cleaved [1273]. The enzyme degrades casein, fibronectin, gelatin, collagen type IV, fibrinogen, and high-molecular-mass kininogen [2047] and is associated with diseases such as ovarian cancer and Alzheimer’s disease [1273]. Belongs in peptidase family S1A.

References: [381, 2303, 2047, 1273]

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**EC 3.4.21.119**

Accepted name: kallikrein 13

Reaction: Hydrolyses mouse Ren2 protein (a species of prorenin present in the submandibular gland) on the carboxy side of the arginine residue at the Lys-Arg pair in the N-terminus, to yield mature renin

Other name(s): KLK13; kallikrein mK13; mGK-13; mK13; mKLK13; prorenin converting enzyme 1; PRECE-1; prorenin-converting enzyme; PRECE; proteinase P

Comments: The enzyme is specific for prorenin from the mouse submandibular gland, as prorenin from the mouse kidney (Ren1) and human prorenin are not substrates [1778]. Site-directed mutagenesis studies have shown that the enzyme will also cleave prorenin when Lys-Arg is replaced by Arg-Arg or Gln-Arg but the rate of reaction is much slower when Lys-Lys is used. This enzyme is also able to process pro-interleukin-1β (pro-IL-1β) in mouse submandibular gland to form IL-1β [2859]. Belongs in peptidase family S1A.

References: [1778, 1263, 1250, 2859]
EC 3.4.21.120

Accepted name: oviductin
Reaction: Preferential cleavage at Gly-Ser-Arg\(^{373}\) of glycoprotein gp43 in *Xenopus laevis* coelomic egg envelope to yield gp41
Other name(s): oviductal protease
Comments: The egg envelope of the South African clawed frog (*Xenopus laevis*) is modified during transit of the egg through the pars rectus oviduct, changing the egg envelope from an unfertilizable form to a fertilizable form. This process involves the conversion of glycoprotein gp43 to gp41 (ZPC) by the pars recta protease oviductin. It is thought that the enzymatically active protease molecule comprises the N-terminal protease domain coupled to two C-terminal CUB domains, which are related to the mammalian spermadhesin molecules implicated in mediating sperm-envelope interactions [1472]. The enzyme is also found in the Japanese toad (*Bufo japonicus*) [1017]. Belongs in peptidase family S1.
References: [927, 1472, 1017]

EC 3.4.22 Cysteine endopeptidases

EC 3.4.22.1

Accepted name: cathepsin B
Reaction: Hydrolysis of proteins with broad specificity for peptide bonds. Preferentially cleaves -Arg-Arg bonds in small molecule substrates (thus differing from cathepsin L). In addition to being an endopeptidase, shows peptidyl-dipeptidase activity, liberating C-terminal dipeptides
Other name(s): cathepsin B1 (obsolete); cathepsin II
Comments: An intracellular (lysosomal) enzyme in peptidase family C1 (papain family)
References: [236, 141, 1998, 140, 1271]

EC 3.4.22.2

Accepted name: papain
Reaction: Hydrolysis of proteins with broad specificity for peptide bonds, but preference for an amino acid bearing a large hydrophobic side chain at the P2 position. Does not accept Val in P1'
Other name(s): papayotin; summetrin; velardon; papaine; Papaya peptidase I
Comments: Type example of peptidase family C1 from latex of the papaya (*Carica papaya*) fruit. Inhibited by compound E-64 and proteins of the cystatin family.
References: [1190, 1635]

EC 3.4.22.3

Accepted name: ficain
Reaction: Similar to that of papain
Other name(s): ficin; debricin; higueroxy1 delabarre
Comments: The major proteolytic component of the latex of fig, *Ficus glabrata*. Cysteine endopeptidases with similar properties are present in other members of the large genus Ficus. In peptidase family C1 (papain family).
References: [1456, 274]
Transferred entry. bromelain (stem). Now EC 3.4.22.32 (stem bromelain) and EC 3.4.22.33 (fruit bromelain)

[EC 3.4.22.4 created 1972, deleted 1992 [EC 3.4.22.5 created 1972, incorporated 1978]]

Transferred entry. bromelain (juice). Now EC 3.4.22.32 (stem bromelain) and EC 3.4.22.33 (fruit bromelain)

[EC 3.4.22.5 created 1972, deleted 1978]

EC 3.4.22.6
Accepted name: chymopapain
Reaction: Similar to that of papain
Other name(s): chymopapain A; chymopapain B; chymopapain S
Comments: The major endopeptidase of papaya (Carica papaya) latex. It has multiple chromatographic forms. In peptidase family C1 (papain family).
References: [274, 1119, 310]

[EC 3.4.22.6 created 1961 as EC 3.4.4.11, transferred 1972 to EC 3.4.22.6]

EC 3.4.22.7
Accepted name: asclepian
Reaction: Similar to that of papain
Comments: From the latex of milkweed, Asclepias syriaca. It has multiple forms, and is in peptidase family C1 (papain family)
References: [272]

[EC 3.4.22.7 created 1972]

EC 3.4.22.8
Accepted name: clostripain
Reaction: Preferential cleavage: Arg, including Arg-Pro, but not Lys-Pro
Other name(s): clostridiopetidase B; clostridium histolyticum proteinase B; α-clostridipain; clostridiopeptidase
Comments: From the bacterium Clostridium histolyticum. It requires Ca\(^{2+}\) ions and is inhibited by EDTA. Type example of peptidase family C11.
References: [1674, 819, 820]

[EC 3.4.22.8 created 1961 as EC 3.4.4.20, transferred 1972 to EC 3.4.22.8]

Transferred entry. yeast proteinase B. Now EC 3.4.21.48, cerevisin

[EC 3.4.22.9 created 1972, deleted 1981]

EC 3.4.22.10
Accepted name: streptopain
Reaction: Preferential cleavage with hydrophobic residues at P2, P1 and P1' 
Other name(s): Streptococcus peptidase A; streptococcal cysteine proteinase; Streptococcus protease
Comments: From the bacterium, group A Streptococcus. Formed from the proenzyme by limited proteolysis. Type example of peptidase family C10.
References: [619, 1486, 2476, 1490]

[EC 3.4.22.10 created 1961 as EC 3.4.4.18, transferred 1972 to EC 3.4.22.10]

Transferred entry. insulinase. Now EC 3.4.24.56, insulysin

[EC 3.4.22.11 created 1976, deleted 1978 [transferred to EC 3.4.99.45, deleted 1993]]

Transferred entry. γ-glutamyl hydrolase. Now EC 3.4.19.9, γ-glutamyl hydrolase
EC 3.4.22.14
Accepted name: actinidain
Reaction: Similar to that of papain
Other name(s): actinidin; Actinidia anionic protease; proteinase A₂ of Actinidia chinensis
Comments: From the kiwi fruit or Chinese gooseberry (Actinidia chinensis). In peptidase family C1 (papain family)
References: [111, 1190, 112]

[EC 3.4.22.14 created 1978]

EC 3.4.22.15
Accepted name: cathepsin L
Reaction: Similar to that of papain. As compared to cathepsin B, cathepsin L exhibits higher activity towards protein substrates, but has little activity on Z-Arg-Arg-NHMec, and no peptidyl-dipeptidase activity
Other name(s): Aldrichina grahami cysteine proteinase
Comments: A lysosomal enzyme in peptidase family C1 (papain family) that is readily inhibited by the diazomethane inhibitor Z-Phe-Phe-CH₂ or the epoxide inhibitor E-64
References: [141, 140, 1162, 1271]

[EC 3.4.22.15 created 1978 (EC 3.4.99.19 created 1972, incorporated 1981)]

EC 3.4.22.16
Accepted name: cathepsin H
Reaction: Hydrolysis of proteins, acting as an aminopeptidase (notably, cleaving Arg— bonds) as well as an endopeptidase
Other name(s): cathepsin B3; benzoylarginine-naphthylamide (BANA) hydrolase (obsolete); cathepsin Ba, aleurain; N-benzoylarginine-β-naphthylamide hydrolase
Comments: Present in lysosomes of mammalian cells. In peptidase family C1 (papain family)
References: [141, 277, 743]

[EC 3.4.22.16 created 1981, modified 1989]

[3.4.22.17 Transferred entry. calpain. Now EC 3.4.22.53, calpain-2]
[EC 3.4.22.17 created 1981 [EC 3.4.24.5 created 1978, part incorporated 1989], deleted 2003]

[3.4.22.18 Transferred entry. prolyl endopeptidase (thiol-dependent). Now EC 3.4.21.26, prolyl oligopeptidase]
[EC 3.4.22.18 created 1981, deleted 1992]

[3.4.22.19 Transferred entry. endo-oligopeptidase. Now EC 3.4.24.15, thimet oligopeptidase]
[EC 3.4.22.19 created 1989, deleted 1992]

[3.4.22.20 Deleted entry. dinorphin-converting enzyme]
[EC 3.4.22.20 created 1989, deleted 1992]

[3.4.22.21 Transferred entry. yeast cysteine proteinase E. Now EC 3.4.25.1, proteasome endopeptidase complex]
[EC 3.4.22.21 created 1989, deleted 1992]

[3.4.22.22 Transferred entry. yeast cysteine proteinase D. Now EC 3.4.24.37, saccharolysin]
[EC 3.4.22.22 created 1989, deleted 1992]

3.4.22.23  Transferred entry. yeast cysteine proteinase F. Now EC 3.4.21.61, kexin

[EC 3.4.22.23 created 1989, deleted 1992]

EC 3.4.22.24
Accepted name: cathepsin T
Reaction: Interconversion of the three forms of tyrosine aminotransferase, EC 2.6.1.5
Comments: Degrades azocasein and denatured hemoglobin; the only native protein on which it has been shown to act is tyrosine aminotransferase
References: [836, 835, 1986]

[EC 3.4.22.24 created 1990]

EC 3.4.22.25
Accepted name: glycyl endopeptidase
Reaction: Preferential cleavage: Gly−Ile bond in proteins and small molecule substrates
Other name(s): papaya peptidase B; papaya protease IV; glycine-specific protease; chymopapain; Papaya protease 4; PPIV; chymopapain M
Comments: From the papaya plant, Carica papaya. Not inhibited by chicken cystatin, unlike most other homologues of papain, but in peptidase family C1 (papain family)
References: [1995, 311, 2116, 313, 312]

[EC 3.4.22.25 created 1992]

EC 3.4.22.26
Accepted name: cancer procoagulant
Reaction: Specific cleavage of Arg−Ile bond in Factor X to form Factor Xa
Comments: Apparently produced only by malignant and fetal cells
References: [656, 657]

[EC 3.4.22.26 created 1992]

EC 3.4.22.27
Accepted name: cathepsin S
Reaction: Similar to cathepsin L, but with much less activity on Z-Phe-Arg−NHMec, and more activity on the Z-Val-Val-Arg− compound
Comments: A lysosomal cysteine endopeptidase that is unusual amongst such enzymes for its stability to neutral pH. In peptidase family C1 (papain family)
References: [2631, 281, 1270]

[EC 3.4.22.27 created 1992]

EC 3.4.22.28
Accepted name: picornain 3C
Reaction: Selective cleavage of Gln−Gly bond in the poliovirus polyprotein. In other picornavirus reactions Glu may be substituted for Gln, and Ser or Thr for Gly
Other name(s): picornavirus endopeptidase 3C; poliovirus protease 3C; rhinovirus protease 3C; foot-and-mouth protease 3C; poliovirus proteinase 3C; rhinovirus proteinase 3C; coxsackievirus 3C proteinase; foot-and-mouth-disease virus proteinase 3C; 3C protease; 3C proteinase; cysteine proteinase 3C; hepatitis A virus 3C proteinase; protease 3C; tomato ringspot nepovirus 3C-related protease
Comments: From entero-, rhino-, aphi- and cardioviruses. Larger than the homologous virus picornain 2A. Type example of peptidase family C3

[EC 3.4.22.28 created 1992]
EC 3.4.22.29

Accepted name: picornain 2A
Reaction: Selective cleavage of Tyr-Gly bond in picornavirus polyprotein
Other name(s): picornavirus endopeptidase 2A; poliovirus protease 2A; rhinovirus protease 2A; 2A proteinase; protease 2A; proteinase 2Apro; picornaviral 2A proteinase; Y-G proteinase 2A; poliovirus proteinase 2A; poliovirus protease 2Apro; picornaviral 2A proteinase
Comments: From entero-, rhino-, aphto- and cardioviruses. Smaller than the homologous picornain 3C, which is also in peptidase family C3 (picornain 3C family)
References: [1107, 157, 1326, 1804]

EC 3.4.22.30

Accepted name: caricain
Reaction: Hydrolysis of proteins with broad specificity for peptide bonds, similar to those of papain and chymopapain
Other name(s): papaya peptidase A; papaya peptidase II; papaya proteinase ; papaya proteinase III; papaya proteinase 3; proteinase ω; papaya proteinase A; chymopapain S; Pp
Comments: From papaya plant, Carica papaya. In peptidase family C1 (papain family)
References: [2228, 2128, 1996, 273, 2929, 587]

EC 3.4.22.31

Accepted name: ananain
Reaction: Hydrolysis of proteins with broad specificity for peptide bonds. Best reported small molecule substrate Bz-Phe-Val-Arg-NHMec, but broader specificity than fruit bromelain
Other name(s): stem bromelain; fruit bromelain
Comments: From stem of pineapple plant, Ananas comosus. Differs from stem and fruit bromelains in being inhibited by chicken cystatin. In peptidase family C1 (papain family)
References: [2154, 2155]

EC 3.4.22.32

Accepted name: stem bromelain
Reaction: Broad specificity for cleavage of proteins, but strong preference for Z-Arg-Arg-NHMec amongst small molecule substrates
Other name(s): bromelain; pineapple stem bromelain
Comments: The most abundant of the cysteine endopeptidases of the stem of the pineapple plant, Ananas comosus. Distinct from the bromelain found in the pineapple fruit (EC 3.4.22.33). Scarcely inhibited by chicken cystatin and also very slowly inactivated by E-64. In peptidase family C1 (papain family)
References: [274, 2154, 2117, 2155]

EC 3.4.22.33

Accepted name: fruit bromelain
Reaction: Hydrolysis of proteins with broad specificity for peptide bonds. Bz-Phe-Val-Arg-NHMe is a good synthetic substrate, but there is no action on Z-Arg-Arg-NHMe (c.f. stem bromelain)

Other name(s): juice bromelain; ananase; bromelase; bromelin; extranase; juice bromelain; pinase; pineapple enzyme; traumanase; fruit bromelain FA2

Comments: From the pineapple plant, Ananas comosus. Scarcely inhibited by chicken cystatin. Another cysteine endopeptidase, with similar action on small molecule substrates, pinguinain, is obtained from the related plant, Bromelia pinguin, but pinguinain differs from fruit bromelain in being inhibited by chicken cystatin [2155].

References: [2212, 2841, 1916, 2155]

[EC 3.4.22.33 created 1965 as EC 3.4.4.24, transferred 1972 to EC 3.4.22.4, part transferred 1992 to EC 3.4.22.33]

EC 3.4.22.34
Accepted name: legumain
Reaction: Hydrolysis of proteins and small molecule substrates at -Asn-Xaa- bonds
Other name(s): asparaginyl endopeptidase; citvac; proteinase B (ambiguous); hemoglobinase (ambiguous); PRSC1 gene product (Homo sapiens); vicilin peptidohydrolase; bean endopeptidase; vicilin peptidohydrolase
Comments: Best known from legume seeds, the trematode Schistosoma mansoni and mammalian lysosomes. Not inhibited by compound E-64. Type example of peptidase family C13
References: [924, 473, 374]

[EC 3.4.22.34 created 1992, modified 2000]

EC 3.4.22.35
Accepted name: histolysain
Reaction: Hydrolysis of proteins, including basement membrane collagen and azocasein. Preferential cleavage: Arg-Arg in small molecule substrates including Z-Arg-Arg-NHMe
Other name(s): histolysin; histolysin; Entamoeba histolytica cysteine proteinase; amebapain; Entamoeba histolytica cysteine protease; Entamoeba histolytica neutral thiol proteinase
Comments: From the protozoan, Entamoeba histolytica. In peptidase family C1 (papain family)
References: [1514, 1505]

[EC 3.4.22.35 created 1992]

EC 3.4.22.36
Accepted name: caspase-1
Reaction: Strict requirement for an Asp residue at position P1 and has a preferred cleavage sequence of Tyr-Val-Ala-Asp
Other name(s): interleukin 1β-converting enzyme; protease VII; protease A; interleukin 1β precursor proteinase; interleukin 1 converting enzyme; interleukin 1β-converting endopeptidase; interleukin-1β convertase; interleukin-1β converting enzyme; interleukin-1β precursor proteinase; prointerleukin 1β protease; precursor interleukin-1β converting enzyme; pro-interleukin 1β proteinase; ICE
Comments: From mammalian monocytes. This enzyme is part of the family of inflammatory caspases, which also includes caspase-4 (EC 3.4.22.57) and caspase-5 (EC 3.4.22.58) in humans and caspase-11 (EC 3.4.22.64), caspase-12, caspase-13 and caspase-14 in mice. Contains a caspase-recruitment domain (CARD) in its N-terminal prodomain, which plays a role in procaspase activation [1578, 358]. Cleaves pro-interleukin-1β (pro-IL-1β) to form mature IL-1β, a potent mediator of inflammation. Also activates the proinflammatory cytokine, IL-18, which is also known as interferon-γ-inducing factor [1578]. Inhibited by Ac-Tyr-Val-Ala-Asp-CHO. Caspase-11 plays a critical role in the activation of caspase-1 in mice, whereas caspase-4 enhances its activation in humans [358]. Belongs in peptidase family C14.
References: [1048, 2560, 2559, 36, 1563, 1578, 358]

[EC 3.4.22.36 created 1993, modified 1997, modified 2007]
EC 3.4.22.37
Accepted name: gingipain R
Reaction: Hydrolysis of proteins and small molecule substrates, with a preference for Arg in P1
Other name(s): Arg-gingipain; gingipain-1; argingipain; Arg-gingivain-55 proteinase; Arg-gingivain-70 proteinase; Arg-gingivain-75 proteinase; arginine-specific cysteine protease; arginine-specific gingipain; arginine-specific gingivain; RGP-1; RGP
Comments: A secreted endopeptidase from the bacterium *Porphyromonas gingivalis*. Strongly activated by glycine [380], and stabilized by Ca$^{2+}$. Precursor molecule contains a hemagglutinin domain [1272, 1951]. Misleadingly described in some literature as "trypsin-like", being a cysteine peptidase, type example of family C25
References: [380, 1272, 1951]

[EC 3.4.22.37 created 1996]

EC 3.4.22.38
Accepted name: cathepsin K
Reaction: Broad proteolytic activity. With small-molecule substrates and inhibitors, the major determinant of specificity is P2, which is preferably Leu, Met > Phe, and not Arg
Other name(s): cathepsin O and cathepsin X (both misleading, having been used for other enzymes); cathepsin O2
Comments: Prominently expressed in mammalian osteoclasts, and believed to play a role in bone resorption. In peptidase family C1 (papain family)
References: [1088, 245, 278, 2914, 1621]

[EC 3.4.22.38 created 1997]

EC 3.4.22.39
Accepted name: adenain
Reaction: Cleaves proteins of the adenovirus and its host cell at two consensus sites: -Yaa-Xaa-Gly-Gly- and -Yaa-Xaa-Gly- (in which Yaa is Met, Ile or Leu, and Xaa is any amino acid)
Comments: A cysteine endopeptidase from adenoviruses, the type example of peptidase family C5, with a protein fold unlike that known for any other peptidase [549]. Activity is greatly stimulated by the binding to the enzyme of an 11-residue peptide from the adenovirus capsid protein pre-VI at a site separate from the active site [2762]
References: [2762, 549, 2761]

[EC 3.4.22.39 created 2000]

EC 3.4.22.40
Accepted name: bleomycin hydrolase
Reaction: Inactivates bleomycin B2 (a cytotoxic glycometallopeptide) by hydrolysis of a carboxyamide bond of β-aminoalanine, but also shows general aminopeptidase activity. The specificity varies somewhat with source, but amino acid arylamides of Met, Leu and Ala are preferred [1]
Other name(s): aminopeptidase C (*Lactococcus lactis*) [4]
Comments: The molecule is a homohexamer in which the monomers have a papain-like tertiary structure (in peptidase family C1). The active sites are on the walls of a central channel through the molecule, and access of substrate molecules to them is obstructed by this and by the C-terminus of each polypeptide chain [2916]. Bleomycin can scarcely be the natural substrate, and there are reports of limited endopeptidase activity. Known from bacteria as well as eukaryotic organisms. Hydrolase H from chicken muscle has many similarities to bleomycin hydrolase, but hydrolyses Ph-CO-Arg-2-naphthylamine as well as aminopeptidase substrates [14].
References: [280, 14, 2916, 1672]

[EC 3.4.22.40 created 2000]
EC 3.4.22.41
Accepted name: cathepsin F
Reaction: The recombinant enzyme cleaves synthetic substrates with Phe and Leu (better than Val) in P2, with high specificity constant ($k_{cat}/K_m$) comparable to that of cathepsin L
Comments: Cathepsin F is a lysosomal cysteine endopeptidase of family C1 (papain family), most active at pH 5.9. The enzyme is unstable at neutral pH values and is inhibited by compound E-64. Cathepsin F is expressed in most tissues of human, mouse and rat. Human gene locus: 11q13.1-13.3
References: [2204, 1757, 2782, 2730]

EC 3.4.22.42
Accepted name: cathepsin O
Reaction: The recombinant human enzyme hydrolyses synthetic endopeptidase substrates including Z-Phe-Arg-NHMec and Z-Arg-Arg-NHMec
Comments: Cathepsin O is a lysosomal cysteine peptidase of family C1 (papain family). The recombinant human enzyme is catalytically active at pH 6.0 and is inhibited by compound E-64. Cathepsin O is ubiquitously expressed in human tissues and the human gene locus is 4q31-32
References: [2202, 2686]

EC 3.4.22.43
Accepted name: cathepsin V
Reaction: The recombinant enzyme hydrolysates proteins (serum albumin, collagen) and synthetic substrates (Z-Phe-Arg-NHMec > Z-Leu-Arg-NHMec > Z-Val-Arg-NHMec)
Other name(s): Cathepsin L2; cathepsin U
Comments: Cathepsin V is a human lysosomal cysteine endopeptidase of family C1 (papain family) that is maximally active at pH 5.7 and unstable at neutral pH. Compound E-64, leupeptin and chicken cystatin are inhibitors. Human cathepsin V shows expression restricted to thymus, testis, corneal epithelium and some colon and breast carcinomas. Human gene locus: 9q22.2
References: [279, 15, 2203]

EC 3.4.22.44
Accepted name: nuclear-inclusion-a endopeptidase
Reaction: Hydrolyses glutaminyl bonds, and activity is further restricted by preferences for the amino acids in P6 - P1' that vary with the species of potyvirus, e.g. Glu-Xaa-Xaa-Tyr-Xaa-Gln-(Ser or Gly) for the enzyme from tobacco etch virus. The natural substrate is the viral polyprotein, but other proteins and oligopeptides containing the appropriate consensus sequence are also cleaved.
Other name(s): potyvirus NIa protease
Comments: The potyviruses cause diseases in plants, and inclusion bodies appear in the host cell nuclei; protein a of the inclusion bodies is the endopeptidase. The enzyme finds practical use when encoded in vectors for the artificial expression of recombinant fusion proteins, since it can confer on them the capacity for autolytic cleavage. It is also reported that transgenic plants expressing the enzyme are resistant to viral infection. Type example of peptidase family C4.
References: [675, 1254, 2489, 1257]

EC 3.4.22.45
Accepted name: helper-component proteinase
Reaction: Hydrolyses a Gly—Gly bond at its own C-terminus, commonly in the sequence -Tyr-Xaa-Val-Gly—Gly, in the processing of the potyviral polyprotein.

Other name(s): HC-Pro

Comments: Known from many potyviruses. The helper component-proteinase of the tobacco etch virus is a multifunctional protein with several known activities: the N-terminal region is required for aphid transmission and efficient genome amplification, the central region is required for long-distance movement in plants, and the C-terminal domain has cysteine endopeptidase activity. Type example of peptidase family C6.

References: [1207, 2687]

[EC 3.4.22.45 created 2001]

EC 3.4.22.46

Accepted name: L-peptidase

Reaction: Autocatalytically cleaves itself from the polyprotein of the foot-and-mouth disease virus by hydrolysis of a Lys—Gly bond, but then cleaves host cell initiation factor eIF-4G at bonds -Gly—Arg- and -Lys—Arg-.

Comments: Best known from foot-and-mouth disease virus, but occurs in other aphthoviruses and cardioviruses. Destruction of initiation factor eIF-4G has the effect of shutting off host-cell protein synthesis while allowing synthesis of viral proteins to continue. The tertiary structure reveals a distant relationship to papain and, consistent with this, compound E-64 is inhibitory. Type example of peptidase family C28.

References: [1974, 885]

[EC 3.4.22.46 created 2001]

EC 3.4.22.47

Accepted name: gingipain K

Reaction: Endopeptidase with strict specificity for lysyl bonds

Other name(s): Lys-gingipain; PrtP proteinase

Comments: Activity is stimulated by glycine. Known from the bacterium Porphyromonas gingivalis and contributes to the pathogenicity of the organism. In peptidase family C25.

References: [1982, 467]

[EC 3.4.22.47 created 2003]

EC 3.4.22.48

Accepted name: staphopain

Reaction: Broad endopeptidase action on proteins including elastin, but rather limited hydrolysis of small-molecule substrates. Assays are conveniently made with hemoglobin, casein or Z-Phe-Arg-NHMec as substrate

Other name(s): staphylopain

Comments: Known from species of Staphylococcus. Type example of peptidase family C47.

References: [1021, 2009, 586]

[EC 3.4.22.48 created 2003]

EC 3.4.22.49

Accepted name: separase

Reaction: All bonds known to be hydrolysed by this endopeptidase have arginine in P1 and an acidic residue in P4. P6 is often occupied by an acidic residue or by an hydroxy-amino-acid residue, the phosphorylation of which enhances cleavage

Other name(s): separin
In both budding yeast and human cells, cleavage of the cohesin subunit Scc1 by separase is required for sister chromatid separation in mitosis. Budding yeast separase is also known to cleave the Rec8 subunit of a meiotic cohesin complex and the kinetochore protein Slk19. Type example of peptidase family C50.

References: [2711]

[EC 3.4.22.49 created 2003]

EC 3.4.22.50
Accepted name: V-cath endopeptidase
Reaction: Endopeptidase of broad specificity, hydrolyzing substrates of both cathepsin L and cathepsin B
Other name(s): AcNPV protease; BmNPV protease; NPV protease; baculovirus cathepsin; nucleopolyhedrosis virus protease; viral cathepsin
Comments: In peptidase family C1. Contributes to the liquefaction of the tissues of the insect host in the late stages of infection by the baculovirus.
References: [2358, 956]

[EC 3.4.22.50 created 2003]

EC 3.4.22.51
Accepted name: cruzipain
Reaction: Broad endopeptidase specificity similar to that of cathepsin L
Other name(s): congopain; cruzain; evansain; trypanopain
Comments: In peptidase family C1. Is located in the digestive vacuoles of the parasitic trypanosome and contributes to the nutrition of the organism by digestion of host proteins.
References: [350]

[EC 3.4.22.51 created 2003]

EC 3.4.22.52
Accepted name: calpain-1
Reaction: Broad endopeptidase specificity
Other name(s): µ-calpain; calcium-activated neutral protease I
Comments: In peptidase family C2. Requires Ca²⁺ at micromolar concentrations for activity. Cytosolic in animal cells. The active enzyme molecule is a heterodimer in which the large subunit contains the peptidase unit, and the small subunit is also a component of EC 3.4.22.53, calpain-2.
References: [600]

[EC 3.4.22.52 created 1981 as EC 3.4.22.17, transferred 2003 to EC 3.4.22.52]

EC 3.4.22.53
Accepted name: calpain-2
Reaction: Broad endopeptidase specificity
Other name(s): calcium-activated neutral protease II; m-calpain; milli-calpain
Comments: Type example of peptidase family C2. Requires Ca²⁺ at millimolar concentrations for activity. Cytosolic in animal cells. The active enzyme molecule is a heterodimer in which the large subunit contains the peptidase unit, and the small subunit is also a component of EC 3.4.22.52, calpain-1.
References: [2436, 600]

[EC 3.4.22.53 created 1981 as EC 3.4.22.17, transferred 2003 to EC 3.4.22.53]

EC 3.4.22.54
**Accepted name:** calpain-3  
**Reaction:** Broad endopeptidase activity  
**Other name(s):** p94; calpain p94; CAPN3; muscle calpain; calpain 3; calcium-activated neutral proteinase 3; muscle-specific calcium-activated neutral protease 3; CANP 3; calpain L3  
**Comments:** This Ca$^{2+}$-dependent enzyme is found in skeletal muscle and is genetically linked to limb girdle muscular dystrophy type 2A [2391, 535]. The enzyme is activated by autoproteolytic cleavage of insertion sequence 1 (IS1), which allows substrates and inhibitors gain access to the active site [535]. Substrates include the protein itself [2100, 535] and connectin/titin [2392, 1905]. Belongs in peptidase family C2.  
**References:** [2391, 2392, 2100, 535, 1905]  

**EC 3.4.22.55**  
**Accepted name:** caspase-2  
**Reaction:** Strict requirement for an Asp residue at P1, with Asp$^{316}$ being essential for proteolytic activity and has a preferred cleavage sequence of Val-Asp-Val-Ala-Asp$^{\underline{\underline{\underline{316}}}}$.  
**Other name(s):** ICH-1; NEDD-2; caspase-2L; caspase-2S; neural precursor cell expressed developmentally down-regulated protein 2; CASP-2; NEDD2 protein  
**Comments:** Caspase-2 is an initiator caspase, as are caspase-8 (EC 3.4.22.61), caspase-9 (EC 3.4.22.62) and caspase-10 (EC 3.4.22.63) [358]. Contains a caspase-recruitment domain (CARD) in its N-terminal prodomain, which plays a role in procaspase activation [358]. Two forms of caspase-2 with antagonistic effects exist: caspase-2L induces programmed cell death and caspase-2S suppresses cell death [2,3,5]. Caspase-2 is activated by caspase-3 (EC 3.4.22.56), or by a caspase-3-like protease. Activation involves cleavage of the N-terminal prodomain, followed by self-proteolysis between the large and small subunits of pro-caspase-2 and further proteolysis into smaller fragments [1437]. Proteolysis occurs at Asp residues and the preferred substrate for this enzyme is a pentapeptide rather than a tetrapeptide [2917]. Apart from itself, the enzyme can cleave golgin-16, which is present in the Golgi complex and has a cleavage site that is unique for caspase-2 [1551, 2917]. αII-Spectrin, a component of the membrane cytoskeleton, is a substrate of the large isoform of pro-caspase-2 (caspase-2L) but not of the short isoform (caspase-2S). Belongs in peptidase family C14.  
**References:** [1342, 2735, 1437, 1551, 2917, 358]  

**EC 3.4.22.56**  
**Accepted name:** caspase-3  
**Reaction:** Strict requirement for an Asp residue at positions P1 and P4. It has a preferred cleavage sequence of Asp-Xaa-Xaa-Asp$^{\underline{\underline{\underline{\underline{358}}}}}$ with a hydrophobic amino-acid residue at P2 and a hydrophilic amino-acid residue at P3, although Val or Ala are also accepted at this position  
**Other name(s):** CPP32; apopain; yama protein  
**Comments:** Caspase-3 is an effector/executioner caspase, as are caspase-6 (EC 3.4.22.59) and caspase-7 (EC 3.4.22.60) [358]. These caspases are responsible for the proteolysis of the majority of cellular polypeptides [e.g. poly(ADP-ribose) polymerase (PARP)], which leads to the apoptotic phenotype [1802, 358]. Procaspase-3 can be activated by caspase-1 (EC 3.4.22.36), caspase-8 (EC 3.4.22.61), caspase-9 (EC 3.4.22.62) and caspase-10 (EC 3.4.22.63) as well as by the serine protease granzyme B [1328]. Caspase-3 can activate procaspase-2 (EC 3.4.22.55) [1437]. Activation occurs by inter-domain cleavage followed by removal of the N-terminal prodomain [1574]. Although Asp-Glu-(Val/Ile)-Asp is thought to be the preferred cleavage sequence, the enzyme can accommodate different residues at P2 and P3 of the substrate [660]. Like caspase-2, a hydrophobic residue at P5 of caspase-3 leads to more efficient hydrolysis, e.g. (Val/Leu)-Asp-Val-Ala-Asp$^{\underline{\underline{\underline{\underline{358}}}}}$ is a better substrate than Asp-Val-Ala-Asp$^{\underline{\underline{\underline{\underline{358}}}}}$. This is not the case for caspase-7 [660]. Belongs in peptidase family C14.  
**References:** [1328, 1437, 1802, 660, 358, 1574]
EC 3.4.22.57

**Accepted name:** caspase-4

**Reaction:** Strict requirement for Asp at the P1 position. It has a preferred cleavage sequence of Tyr-Val-Ala-Asp but also cleaves at Asp-Glu-Val-Asp.

**Other name(s):** ICErel-II; ICErel-II; Ich-2; transcript X; TX; TX protease; caspase 4; CASP-4

**Comments:** This enzyme is part of the family of inflammatory caspases, which also includes caspase-1 (EC 3.4.22.36) and caspase-5 (EC 3.4.22.58) in humans and caspase-11 (EC 3.4.22.64), caspase-12, caspase-13 and caspase-14 in mice. Contains a caspase-recruitment domain (CARD) in its N-terminal prodomain, which plays a role in procaspase activation [3,5,6]. The enzyme is able to cleave itself and the p30 caspase-1 precursor, but, unlike caspase-1, it is very inefficient at generating mature interleukin-1β (IL-1β) from pro-IL-1β [668, 664]. Both this enzyme and caspase-5 can cleave pro-caspase-3 to release the small subunit (p12) but not the large subunit (p17) [1186]. The caspase-1 inhibitor Ac-Tyr-Val-Ala-Asp-CHO can also inhibit this enzyme, but more slowly [664]. Belongs in peptidase family C14.

**References:** [668, 1187, 1186, 664, 1578, 358]

EC 3.4.22.58

**Accepted name:** caspase-5

**Reaction:** Strict requirement for Asp at the P1 position. It has a preferred cleavage sequence of Tyr-Val-Ala-Asp but also cleaves at Asp-Glu-Val-Asp.

**Other name(s):** ICErel-III; Ich-3; ICH-3 protease; transcript Y; TY; CASP-5

**Comments:** This enzyme is part of the family of inflammatory caspases, which also includes caspase-1 (EC 3.4.22.36) and caspase-4 (EC 3.4.22.57) in humans and caspase-11 (EC 3.4.22.64), caspase-12, caspase-13 and caspase-14 in mice. Contains a caspase-recruitment domain (CARD) in its N-terminal prodomain, which plays a role in procaspase activation [3,5,6]. The enzyme is able to cleave itself and the p30 caspase-1 precursor, but is very inefficient at generating mature interleukin-1β (IL-1β) from pro-IL-1β [667, 664]. Both this enzyme and caspase-4 can cleave pro-caspase-3 to release the small subunit (p12) but not the large subunit (p17) [1186]. Unlike caspase-4, this enzyme can be induced by lipopolysaccharide [1467]. Belongs in peptidase family C14.

**References:** [667, 1186, 1467, 664, 1578, 358]

EC 3.4.22.59

**Accepted name:** caspase-6

**Reaction:** Strict requirement for Asp at position P1 and has a preferred cleavage sequence of Val-Glu-His-Asp.

**Other name(s):** CASP-6; apoptotic protease Mch-2; Mch2

**Comments:** Caspase-6 is an effector/executioner caspase, as are caspase-3 (EC 3.4.22.56) and caspase-7 (EC 3.4.22.60) [358]. These caspases are responsible for the proteolysis of the majority of cellular polypeptides [e.g. poly(ADP-ribose) polymerase (PARP)], which leads to the apoptotic phenotype [358]. Caspase-6 can cleave its prodomain to produce mature caspase-6, which directly activates caspase-8 (EC 3.4.22.61) and leads to the release of cytochrome c from the mitochondria. The release of cytochrome c is an essential component of the intrinsic apoptosis pathway [449]. The enzyme can also cleave and inactivate lamins, the intermediate filament scaffold proteins of the nuclear envelope, leading to nuclear fragmentation in the final phases of apoptosis [2,4,5,6]. Belongs in peptidase family C14.

**References:** [449, 358, 1197, 1405, 1524, 2481]
**EC 3.4.22.60**

**Accepted name:** caspase-7  
**Reaction:** Strict requirement for an Asp residue at position P1 and has a preferred cleavage sequence of Asp-Glu-Val-Asp.  
**Other name(s):** CASP-7; ICE-like apoptotic protease 3; ICE-LAP3; apoptotic protease Mch-3; Mch3; CMH-1  
**Comments:** Caspase-7 is an effector/executioner caspase, as are caspase-3 (EC 3.4.22.56) and caspase-6 (EC 3.4.22.59) [358]. These enzymes are responsible for the proteolysis of the majority of cellular polypeptides [e.g. poly(ADP-ribose) polymerase (PARP)], which leads to the apoptotic phenotype [1802]. Although a hydrophobic residue at P5 of caspase-2 (EC 3.4.22.55) and caspase-3 leads to more efficient hydrolysis, the amino-acid residue at this location in caspase-7 has no effect [660]. Caspase-7 is activated by the initiator caspases [caspase-8 (EC 3.4.22.61), caspase-9 (EC 3.4.22.62) and caspase-10 (EC 3.4.22.63)]. Removal of the N-terminal prodomain occurs before cleavage in the linker region between the large and small subunits [521]. Belongs in peptidase family C14.  
**References:** [358, 1802, 660, 521]  

[EC 3.4.22.60 created 2007]

**EC 3.4.22.61**

**Accepted name:** caspase-8  
**Reaction:** Strict requirement for Asp at position P1 and has a preferred cleavage sequence of (Leu/Asp/Val)-Glu-Thr-Asp→(Gly/Ser/Ala)  
**Other name(s):** FLICE, FADD-like ICE; MACH; MORT1-associated CED-3 homolog; Mch5; mammalian Ced-3 homolog 5; CASP-8; ICE-like apoptotic protease 5; FADD-homologous ICE/CED-3-like protease; apoptotic cysteine protease; apoptotic protease Mch-5; CAP4  
**Comments:** Caspase-8 is an initiator caspase, as are caspase-2 (EC 3.4.22.55), caspase-9 (EC 3.4.22.62) and caspase-10 (EC 3.4.22.63) [358]. Caspase-8 is the apical activator of the extrinsic (death receptor) apoptosis pathway, triggered by death receptor ligation [233]. It contains two tandem death effector domains (DEDs) in its N-terminal prodomain, and these play a role in procaspase activation [358]. This enzyme is linked to cell surface death receptors such as Fas [358, 692]. When Fas is aggregated by the Fas ligand, procaspase-8 is recruited to the death receptor where it is activated [358]. The enzyme has a preference for Glu at P3 and prefers small residues, such as Gly, Ser and Ala, at the P1′ position. It has very broad P4 specificity, tolerating substrates with Asp, Val or Leu in this position [2,3,4]. Endogenous substrates for caspase-8 include procaspase-3, the pro-apoptotic Bcl-2 family member Bid, RIP, PAK2 and the caspase-8 activity modulator FLIP [2194, 692]. Belongs in peptidase family C14.  
**References:** [358, 233, 1743, 2194, 692, 216, 226]  

[EC 3.4.22.61 created 2007]

**EC 3.4.22.62**

**Accepted name:** caspase-9  
**Reaction:** Strict requirement for an Asp residue at position P1 and with a marked preference for His at position P2. It has a preferred cleavage sequence of Leu-Gly-His-Asp→Xaa  
**Other name(s):** CASP-9; ICE-like apoptotic protease 6; ICE-LAP6; apoptotic protease Mch-6; apoptotic protease activating factor 3; APAF-3  
**Comments:** Caspase-9 is an initiator caspase, as are caspase-2 (EC 3.4.22.55), caspase-8 (EC 3.4.22.61) and caspase-10 (EC 3.4.22.63) [358]. Caspase-9 contains a caspase-recruitment domain (CARD) in its N-terminal prodomain, which plays a role in procaspase activation [358]. An alternatively spliced version of caspase-9 also exists, caspase-9S, that inhibits apoptosis, similar to the situation found with caspase-2 [358]. Phosphorylation of caspase-9 from some species by Akt, a serine-threonine protein kinase, inhibits caspase activity in vitro and caspase activation in vivo [358]. The activity of caspase-9 is increased dramatically upon association with the apoptosome but the enzyme can be activated without proteolytic cleavage [2881, 227]. Procaspase-3 is the enzyme’s physiological substrate [2881]. Belongs in peptidase family C14.  
**References:** [358, 2881, 227, 2195]
EC 3.4.22.63

Accepted name: caspase-10

Reaction: Strict requirement for Asp at position P1 and has a preferred cleavage sequence of Leu-Gln-Thr-Asp-Gly

Other name(s): FLICE2, Mch4; CASP-10; ICE-like apoptotic protease 4; apoptotic protease Mch-4; FAS-associated death domain protein interleukin-1β-converting enzyme 2

Comments: Caspase-10 is an initiator caspase, as are caspase-2 (EC 3.4.22.55), caspase-8 (EC 3.4.22.61) and caspase-9 (EC 3.4.22.62) [358]. Like caspase-8, caspase-10 contains two tandem death effector domains (DEDs) in its N-terminal prodomain, and these play a role in procaspase activation [358]. The enzyme has many overlapping substrates in common with caspase-8, such as RIP (the cleavage of which impairs NF-κB survival signalling and starts the cell-death process) and PKA2 (associated with some of the morphological features of apoptosis, such as cell rounding and apoptotic body formation) [692]. Bid, a Bcl2 protein, can be cleaved by caspase-3 (EC 3.4.22.56), caspase-8 and caspase-10 at Lys-Gln-Thr-Asp to yield the pro-apoptotic p15 fragment. The p15 fragment is N-myristoylated and enhances the release of cytochrome c from mitochondria (which, in turn, initiates the intrinsic apoptosis pathway). Bid can be further cleaved by caspase-10 and granzyme B but not by caspase-3 or caspase-8 at Ile-Glu-Thr-Asp to yield a p13 fragment that is not N-myristoylated [692]. Belongs in peptidase family C14.

References: [358, 692, 2301, 226]

EC 3.4.22.64

Accepted name: caspase-11

Reaction: Strict requirement for Asp at the P1 position and has a preferred cleavage sequence of (Ile/Leu/Val/Phe)-Gly-His-Asp

Other name(s): CASP-11

Comments: This murine enzyme is part of the family of inflammatory caspases, which also includes caspase-1 (EC 3.4.22.36), caspase-4 (EC 3.4.22.57) and caspase-5 (EC 3.4.22.58) in humans and caspase-12, caspase-13 and caspase-14 in mice. Contains a caspase-recruitment domain (CARD) in its N-terminal prodomain, which plays a role in procaspase activation. Like caspase-5, but unlike caspase-4, this enzyme can be induced by lipopolysaccharide [1199]. This enzyme not only activates caspase-1, which is required for the maturation of proinflammatory cytokines such as interleukin-1β (IL-1β) and IL-18, but it also activates caspase-3 (EC 3.4.22.56), which leads to cellular apoptosis under pathological conditions [1199, 1061]. Belongs in peptidase family C14.

References: [1199, 1061, 2737, 628, 358]

EC 3.4.22.65

Accepted name: peptidase 1 (mite)

Reaction: Broad endopeptidase specificity

Other name(s): allergen Der f 1; allergen Der p 1; antigen Der p 1; antigen Eur m 1; antigen Pso o 1; major mite fecal allergen Der p 1; Der p 1; Der f 1; Eur m 1; endopeptidase 1 (mite)

Comments: This enzyme, derived from the house dust mite, is a major component of the allergic immune response [1183]. The substrate specificity of this enzyme is not altogether clear. It cleaves the low-affinity IgE receptor CD23 at Glu298-Ser299 and Ser155-Ser156 [1630]. It also cleaves the pulmonary structural proteins occludin and claudin at Leu-Leu, Asp-Leu and at Gly-Thr bonds [1630, 1183]. It can also cleave the α subunit of the interleukin-2 (IL-2) receptor (CD25) [2266]. Using a positional scanning combinatorial library, it was found that the major substrate-specificity determinant is for Ala in the P2 position [934]. The enzyme shows only a slight preference for basic amino acids in the P1 and P3 positions and a preference for aliphatic amino acids such as Ile, Pro, Val, Leu and norleucine in the P4 position [934]. Belongs in peptidase family C1A.
**EC 3.4.22.66**

**Accepted name:** calicivirin  
**Reaction:** Endopeptidase with a preference for cleavage when the P1 position is occupied by Glu and the P1' position is occupied by Gly.  
**Other name(s):** Camberwell virus processing peptidase; Chiba virus processing peptidase; Norwalk virus processing peptidase; Southampton virus processing peptidase; Southport virus; norovirus virus processing peptidase; calicivirus trypsin-like cysteine protease; calicivirus TCP; calicivirus 3C-like protease; calicivirus endopeptidase; rabbit hemorrhagic disease virus 3C endopeptidase  
**Comments:** Viruses that are members of the Norovirus genus (Caliciviridae family) are a major cause of epidemic acute viral gastroenteritis [1482]. The nonstructural proteins of these viruses are produced by proteolytic cleavage of a large precursor polyprotein, performed by a protease that is incorporated into the polyprotein [1]. Cleavage sites are apparently defined by features based on both sequence and structure since several sites in the polyprotein fulfilling the identified sequence requirements are not cleaved [1648]. The presence of acidic (Asp), basic (Arg), aromatic (Tyr) or aliphatic (Leu) amino acids at the P1' position results in only minor differences in cleavage efficiency, suggesting that steric or conformational constraints may play a role in determining specificity [1648]. Changes to the amino acid at the P2 position do not alter cleavage efficiency [1648, 2812]. Belongs in peptidase family C37.  
**References:** [1648, 2812, 38, 1482, 1483]

**EC 3.4.22.67**

**Accepted name:** zingipain  
**Reaction:** Preferential cleavage of peptides with a proline residue at the P2 position  
**Other name(s):** ginger protease; GP-I; GP-II; ginger protease II (*Zingiber officinale*); zingibain  
**Comments:** This enzyme is found in ginger (*Zingiber officinale*) rhizome and is a member of the papain family. GP-II contains two glycosylation sites. The enzyme is inhibited by some divalent metal ions, such as Hg^{2+}, Cu^{2+}, Cd^{2+} and Zn^{2+} [1886]. Belongs in peptidase family C1.  
**References:** [397, 1886, 398]

**EC 3.4.22.68**

**Accepted name:** Ulp1 peptidase  
**Reaction:** Hydrolysis of the α-linked peptide bond in the sequence Gly-Gly-Ala-Thr-Tyr at the C-terminal end of the small ubiquitin-like modifier (SUMO) propeptide, Smt3, leading to the mature form of the protein. A second reaction involves the formation of an ε-linked peptide bond between the C-terminal glycine of the mature SUMO and the lysine ε-amino group of the target protein.  
**Other name(s):** small ubiquitin-related modifier protein 1 conjugate proteinase; Smt3-protein conjugate proteinase; SUMO isopeptidase; SUMO protease; SUMO-1 conjugate proteinase; Sumo-1 hydrolase; SUMO-1-conjugate protease; SUMO-1-deconjugating enzyme; SUMO-specific protease; SUMO-specific proteinase; Ub-specific protease 1; Ulp1; Ulp1 endopeptidase; Ulp1 protease  
**Comments:** The enzyme from *Sacccharomyces cerevisiae* can also recognize small ubiquitin-like modifier 1 (SUMO-1) from human as a substrate in both SUMO-processing (α-linked peptide bonds) and SUMO-deconjugation (ε-linked peptide bonds) reactions [1,2,3]. Ulp1 has several functions, including an essential role in chromosomal segregation and progression of the cell cycle through the G2/M phase of the cell cycle. Belongs in peptidase family C48.  
**References:** [1461, 1442, 2535, 1443, 1072, 1726]
EC 3.4.22.69

**Accepted name:** SARS coronavirus main proteinase  
**Reaction:** TSAVLQSGFRK-NH₂ and SGVTQGKFKK the two peptides corresponding to the two self-cleavage sites of the SARS 3C-like proteinase are the two most reactive peptide substrates. The enzyme exhibits a strong preference for substrates containing Gln at P1 position and Leu at P2 position.  
**Other name(s):** 3C-like protease; coronavirus 3C-like protease; Mpro; SARS coronavirus 3CL protease; SARS coronavirus main peptidase; SARS coronavirus main protease; SARS-CoV 3CLpro enzyme; SARS-CoV main protease; SARS-CoV Mpro; severe acute respiratory syndrome coronavirus main protease  
**Comments:** SARS coronavirus main protease is the key enzyme in SARS coronavirus replicase polyprotein processing. In peptidase family C30.  
**References:** [832, 659, 24]

[EC 3.4.22.69 created 2009]

EC 3.4.22.70

**Accepted name:** sortase A  
**Reaction:** The enzyme catalyses a cell wall sorting reaction in which a surface protein with a sorting signal containing a LPXTG motif is cleaved between the Thr and Gly residue. The resulting threonine carboxyl end of the protein is covalently attached to a pentaglycine cross-bridge of peptidoglycan.  
**Other name(s):** SrtA; SrtA protein; SrtA sortase  
**Comments:** In peptidase family C60.  
**References:** [2579, 2925, 2037]

[EC 3.4.22.70 created 2009]

EC 3.4.22.71

**Accepted name:** sortase B  
**Reaction:** The enzyme catalyses a cell wall sorting reaction in which a surface protein with a sorting signal containing a NXTN motif is cleaved. The resulting threonine carboxyl end of the protein is covalently attached to a pentaglycine cross-bridge of peptidoglycan.  
**Other name(s):** SrtB  
**Comments:** In peptidase family C60.  
**References:** [2926, 191]

[EC 3.4.22.71 created 2009]

EC 3.4.23 Aspartic endopeptidases

EC 3.4.23.1

**Accepted name:** pepsin A  
**Reaction:** Preferential cleavage: hydrophobic, preferably aromatic, residues in P1 and P1′ positions. Cleaves Phe₁→Val, Gln₄→His, Glu₁₃→Ala, Ala₁₄→Leu, Leu₁₅→Tyr, Tyr₁₆→Leu, Gly₂₃→Phe, Phe²₄→Phe and Phe²₅→Tyr bonds in the B chain of insulin  
**Other name(s):** pepsin; lactated pepsin; pepsin fortior; fundus-pepsin; elixir lactate of pepsin; P I; lactated pepsin elixir; P II; pepsin R; pepsin D  
**Comments:** The predominant endopeptidase in the gastric juice of vertebrates, formed from pepsinogen A by limited proteolysis. Human pepsin A occurs in five molecular forms. Pig pepsin D [1397, 1396] is unphosphorylated pepsin A. Type example of peptidase family A1.  
**References:** [1397, 1396, 710, 1130, 741, 2521, 1994]

[EC 3.4.23.1 created 1961 as EC 3.4.4.1, transferred 1972 to EC 3.4.23.1, modified 1986, modified 1989]
EC 3.4.23.2

**Accepted name:** pepsin B

**Reaction:** Degradation of gelatin; little activity on hemoglobin. Specificity on B chain of insulin more restricted than that of pepsin A; does not cleave at Phe\(^1\)-Val, Gln\(^4\)-His or Gly\(^23\)-Phe.

**Other name(s):** parapepsin I; pig gelatinase

**Comments:** Formed from pig pepsinogen B. In peptidase family A1 (pepsin A family).

**References:** [2168]

[EC 3.4.23.2 created 1961 as EC 3.4.4.2, transferred 1972 to EC 3.4.23.2, modified 1986]

EC 3.4.23.3

**Accepted name:** gastricsin

**Reaction:** More restricted specificity than pepsin A, but shows preferential cleavage at Tyr\(\rightarrow\) bonds. High activity on hemoglobin

**Other name(s):** pepsin C; pig parapepsin II; parapepsin II

**Comments:** Formed from progastricsin, apparently in the gastric juice of most vertebrates. In addition to the fundus, progastricsin is also secreted in antrum and proximal duodenum. Seminal plasma contains a zymogen that is immunologically identical with progastricsin [2090]. In peptidase family A1 (pepsin A family).

**References:** [2168, 2520, 708, 709, 1573, 2090, 962]

[EC 3.4.23.3 created 1965 as EC 3.4.4.22, transferred 1972 to EC 3.4.23.3, modified 1986]

EC 3.4.23.4

**Accepted name:** chymosin

**Reaction:** Broad specificity similar to that of pepsin A. Clots milk by cleavage of a single Ser-Phe\(^{105}\)+Met-Ala bond in \(\kappa\)-chain of casein

**Other name(s):** rennin (but this should be avoided since it leads to confusion with rennin)

**Comments:** Neonatal gastric enzyme with high milk clotting and weak general proteolytic activity, formed from prochymosin. Found among mammals with postnatal uptake of immunoglobulins. In peptidase family A1 (pepsin A family).

**References:** [707, 937, 2697]

[EC 3.4.23.4 created 1961 as EC 3.4.4.3, transferred 1972 to EC 3.4.23.4, modified 1986]

EC 3.4.23.5

**Accepted name:** cathepsin D

**Reaction:** Specificity similar to, but narrower than, that of pepsin A. Does not cleave the Gln\(^4\)-His bond in B chain of insulin

**Comments:** Occurs intracellularly, in lysosomes. A zymogen form is known [429]. In peptidase family A1 (pepsin A family).

**References:** [136, 2492, 672, 429]

[EC 3.4.23.5 created 1965 as EC 3.4.4.23, transferred 1972 to EC 3.4.23.5, modified 1986]

[3.4.23.6 Transferred entry. now EC 3.4.23.30 pycnoporopepsin]

[EC 3.4.23.6 created 1961 as EC 3.4.4.17, transferred 1972 to EC 3.4.23.6, modified 1981, deleted 1992 [EC 3.4.23.7, EC 3.4.23.8, EC 3.4.23.9, EC 3.4.23.10, EC 3.4.99.1, EC 3.4.99.15 and EC 3.4.99.25 all created 1972 and incorporated 1978]]

[3.4.23.7 Transferred entry. Penicillium janthinellum acid proteinase. Now EC 3.4.23.20, penicillopepsin]

[EC 3.4.23.7 created 1972, modified 1981, deleted 1978 [transferred to EC 3.4.23.6, deleted 1992]]

[3.4.23.8 Transferred entry. yeast proteinase A. Now EC 3.4.23.25, saccharopepsin]
3.4.23.9 Transferred entry. Rhizopus acid proteinase. Now EC 3.4.23.21, rhizopuspepsin

3.4.23.10 Transferred entry. Endothia acid proteinase. Now EC 3.4.23.22, endothiapepsin

3.4.23.11 Deleted entry. thyroid aspartic proteinase

EC 3.4.23.12

Accepted name: nepenthesin

Reaction: Similar to pepsin, but also cleaves on either side of Asp and at Lys→Arg

Other name(s): Nepenthes aspartic proteinase; Nepenthes acid proteinase; nepenthacin; nepenthasin; aspartyl endopeptidase

Comments: From the insectivorous plants Nepenthes spp. (secretions) and Drosera peltata (ground-up leaves). Aspartic endopeptidases are probably present in many other plants, including Lotus [2307] and sorghum [782]. In peptidase family A1 (pepsin A family)

References: [42, 782, 2307, 41, 2484, 2569]

3.4.23.13 Deleted entry. Lotus aspartic proteinase

3.4.23.14 Deleted entry. sorghum aspartic proteinase

EC 3.4.23.15

Accepted name: renin

Reaction: Cleavage of Leu→ bond in angiotensinogen to generate angiotensin I

Other name(s): angiotensin-forming enzyme; angiotensinogenase

Comments: Formed from prorenin in plasma and kidney. In peptidase family A1 (pepsin A family)

References: [1087, 2359, 1086, 2322]

EC 3.4.23.16

Accepted name: HIV-1 retropepsin

Reaction: Specific for a P1 residue that is hydrophobic, and P1′ variable, but often Pro

Other name(s): human immunodeficiency virus type 1 protease; gag protease; HIV aspartyl protease; HIV proteinase; retroproteinase; HIV-1 protease; HIV-2 protease

Comments: Present in human immunodeficiency virus type 1. Contributes to the maturation of the viral particle, and is a target of antiviral drugs. Active enzyme is a dimer of identical 11-kDa subunits. Similar enzymes occur in other retroviruses [1351]. Type example of peptidase family A2

References: [1351, 596]

EC 3.4.23.17

Accepted name: pro-opiomelanocortin converting enzyme
Reaction: Cleavage at paired basic residues in certain prohormones, either between them, or on the carboxyl side
Other name(s): prohormone converting enzyme; pro-opiomelanocortin-converting enzyme; proopiomelanocortin proteinase; PCE
Comments: A 70 kDa membrane-bound enzyme isolated from cattle pituitary secretory vesicle.
References: [1494, 1493, 646]

EC 3.4.23.18
Accepted name: aspergillopepsin I
Reaction: Hydrolysis of proteins with broad specificity. Generally favours hydrophobic residues in P1 and P1′, but also accepts Lys in P1, which leads to activation of trypsinogen. Does not clot milk
Other name(s): Aspergillus acid protease; Aspergillus acid proteinase; Aspergillus aspartic proteinase; Aspergillus awamori acid proteinase; Aspergillus carboxyl proteinase; Aspergillus kawachii aspartic proteinase; Aspergillus saitoi acid proteinase; sumizyme AP; proctase P; denapsin; denapsin XP 271; proctase
Comments: Found in a variety of Aspergillus species (imperfect fungi): Aspergillus awamori (awamorin, aspergillopepsin A: [1915]), A. fumigatus [1935], A. kawachii [2839], A. niger (proteinase B, proctase B: [1704, 361]), A. oryzae (trypsinogen kinase: [485, 1539]), A. saitoi (aspergillopeptidase A: [1539]), and A. sojae [2513, 1539]. In peptidase family A1 (pepsin A family). Formerly included in EC 3.4.23.6
References: [1320, 1704, 485, 361, 2513, 1914, 1935, 1915, 2839, 1539]

EC 3.4.23.19
Accepted name: aspergillopepsin II
Reaction: Preferential cleavage in B chain of insulin: Asn^3→Gln, Gly^13→Ala, Tyr^28→Thr
Other name(s): proteinase A; Aspergillus niger var. macrosporus aspartic proteinase
Comments: Isolated from Aspergillus niger var. macrosporus, distinct from proteinase B (see aspergillopepsin I) in specificity and insensitivity to pepstatin. In peptidase family A4 (scytalidopepsin B family). Formerly included in EC 3.4.23.6
References: [361, 1073]

EC 3.4.23.20
Accepted name: penicillopepsin
Reaction: Hydrolysis of proteins with broad specificity similar to that of pepsin A, preferring hydrophobic residues at P1 and P1′, but also cleaving Gly^20→Glu in the B chain of insulin. Clots milk, and activates trypsinogen
Other name(s): peptidase A; Penicillium janthinellum aspartic proteinase; acid protease A; Penicillium citrinum acid proteinase; Penicillium cyclopium acid proteinase; Penicillium expansum acid proteinase; Penicillium janthinellum acid proteinase; Penicillium expansum aspartic proteinase; Penicillium aspartic proteinase; Penicillium caseicolum aspartic proteinase; Penicillium roqueforti acid proteinase; Penicillium duponti aspartic proteinase; Penicillium citrinum aspartic proteinase
Comments: From the imperfect fungus Penicillium janthinellum. In peptidase family A1 (pepsin A family). Closely related enzymes have been isolated from P. roqueforti [2910] and P. duponti [623].
EC 3.4.23.21

Accepted name: rhizopuspepsin

Reaction: Hydrolysis of proteins with broad specificity similar to that of pepsin A, preferring hydrophobic residues at P1 and P1′. Clots milk and activates trypsinogen. Does not cleave Gln4-His, but does cleave His10-+Leu and Val12-+Glu in B chain of insulin

Other name(s): Rhizopus aspartic protease; neurase; Rhizopus acid protease; Rhizopus acid proteinase

Comments: From the zygomycete fungus Rhizopus chinensis. A similar endopeptidase is found in R. niveus [1364]. In peptidase family A1 (pepsin A family).

References: [2615, 1364, 1887, 2444]

EC 3.4.23.22

Accepted name: endothiapepsin

Reaction: Hydrolysis of proteins with specificity similar to that of pepsin A; prefers hydrophobic residues at P1 and P1′, but does not cleave Ala14-Leu in the B chain of insulin or Z-Glu-Tyr. Clots milk

Other name(s): Endothia aspartic protease; Endothia acid protease; Endothia parasitica acid protease; Endothia parasitica aspartic proteinase

Comments: From the ascomycete Endothia parasitica. In peptidase family A1 (pepsin A family).

References: [2788, 2804, 127, 437]

EC 3.4.23.23

Accepted name: mucorpepsin

Reaction: Hydrolysis of proteins, favouring hydrophobic residues at P1 and P1′. Clots milk. Does not accept Lys at P1, and hence does not activate trypsinogen

Other name(s): Mucor rennin; Mucor aspartic protease; Mucor acid protease; Mucor miehei aspartic protease; Mucor miehei aspartic protease; Mucor aspartic protease; Mucor pusillus emporase; Fromase 100; Mucor pusillus rennin; Fromase 46TL; Mucor miehei rennin

Comments: Isolated from the zygomycete fungi Mucor pusillus and M. miehei. The two species variants show 83% sequence identity and are immunologically crossreactive. In peptidase family A1 (pepsin A family). Formerly included in EC 3.4.23.6

References: [66, 1919, 2422, 1890, 151]

EC 3.4.23.24

Accepted name: candidapepsin

Reaction: Preferential cleavage at the carboxyl of hydrophobic amino acids, but fails to cleave Leu15-Tyr, Tyr16-Leu and Phe24-Phe of insulin B chain. Activates trypsinogen, and degrades keratin

References: [1536, 2910, 623, 1023, 1052]
**Other name(s):** Candida albicans aspartic proteinase; Candida albicans carboxyl proteinase; Candida albicans secretory acid proteinase; Candida olea acid proteinase; Candida aspartic proteinase; Candida olea aspartic proteinase

**Comments:** This endopeptidase from the imperfect yeast Candida albicans is inhibited by pepstatin, but not by methyl 2-diazoacetamidohexanoate or 1,2-epoxy-3-(p-nitrophenoxy)propane. In peptidase family A1 (pepsin A family). Formerly included in EC 3.4.23.6

**References:** [2094, 2161, 1792, 1499]

[EC 3.4.23.24 created 1992 (EC 3.4.23.6 created 1992 (EC 3.4.23.6 created 1961 as EC 3.4.4.17, transferred 1972 to EC 3.4.23.6, modified 1981 [EC 3.4.23.7, EC 3.4.23.8, EC 3.4.23.9, EC 3.4.23.10, EC 3.4.99.1, EC 3.4.99.15 and EC 3.4.99.25 all created 1972 and incorporated 1978], part incorporated 1992])

**EC 3.4.23.25**

**Accepted name:** saccharopepsin

**Reaction:** Hydrolysis of proteins with broad specificity for peptide bonds. Cleaves -Leu-Leu+Val-Tyr bond in a synthetic substrate. Does not act on esters of Tyr or Arg

**Other name(s):** yeast endopeptidase A; Saccharomyces aspartic proteinase; aspartic proteinase yscA; proteinase A; proteinase yscA; yeast proteinase A; Saccharomyces cerevisiae aspartic proteinase A; yeast proteinase A; PRA

**Comments:** Located in the vacuole of the baker’s yeast (Saccharomyces cerevisiae) cell. In peptidase family A1 (pepsin A family).

**References:** [948, 1644, 45]

[EC 3.4.23.25 created 1992 (EC 3.4.23.6 created 1992 (EC 3.4.23.6 created 1961 as EC 3.4.4.17, transferred 1972 to EC 3.4.23.6, modified 1981 [EC 3.4.23.7, EC 3.4.23.8, EC 3.4.23.9, EC 3.4.23.10, EC 3.4.99.1, EC 3.4.99.15 and EC 3.4.99.25 all created 1972 and incorporated 1978], part incorporated 1992])

**EC 3.4.23.26**

**Accepted name:** rhodotorulapepsin

**Reaction:** Specificity similar to that of pepsin A. Cleaves Z-Lys+Ala-Ala-Ala and activates trypsinogen

**Other name(s):** Cladosporium proteinase; Cladosporium acid proteinase; Paecilomyces proteinase; Rhodotorula glutinis aspartic proteinase; Rhodotorula glutinis acid proteinase

**Comments:** From the imperfect yeast Rhodotorula glutinis. Somewhat similar enzymes have been isolated from the imperfect yeast-like organism Cladosporium sp. [1737, 1848] and the imperfect fungus Paecilomyces varioti [2219, 2220].

**References:** [2219, 2220, 1185, 1737, 1849, 1848, 2483, 1539]

[EC 3.4.23.26 created 1992 (EC 3.4.23.6 created 1992 (EC 3.4.23.6 created 1961 as EC 3.4.4.17, transferred 1972 to EC 3.4.23.6, modified 1981 [EC 3.4.23.7, EC 3.4.23.8, EC 3.4.23.9, EC 3.4.23.10, EC 3.4.99.1, EC 3.4.99.15 and EC 3.4.99.25 all created 1972 and incorporated 1978], part incorporated 1992])

**3.4.23.27** Transferred entry. phasaropepsin. Now EC 3.4.21.103, phasarolisin

[EC 3.4.23.27 created 1992 (EC 3.4.23.6 created 1992 (EC 3.4.23.6 created 1961 as EC 3.4.4.17, transferred 1972 to EC 3.4.23.6, modified 1981 [EC 3.4.23.7, EC 3.4.23.8, EC 3.4.23.9, EC 3.4.23.10, EC 3.4.99.1, EC 3.4.99.15 and EC 3.4.99.25 all created 1972 and incorporated 1978], part incorporated 1992), deleted 2003]

**EC 3.4.23.28**

**Accepted name:** acrocylindropepsin

**Reaction:** Preference for hydrophobic residues at P1 and P1′. Action on the B chain of insulin is generally similar to that of pepsin A, but it also cleaves Leu⁶+Cys(SO₃H), Glu²¹+Arg and Asn⁴+Gln, although not Gln⁴-His

**Other name(s):** Acrocylindrium proteinase; Acrocylindrium acid proteinase

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**Comments:** From the imperfect fungus *Acrocylindrium* sp. Has a very low pH optimum on casein of 2.0. In peptidase family A1 (pepsin A family).

**References:** [2636, 1069, 2483]

[EC 3.4.23.28 created 1992 (EC 3.4.23.6 created 1992 (EC 3.4.23.6 created 1961 as EC 3.4.4.17, transferred 1972 to EC 3.4.23.6, modified 1981 [EC 3.4.23.7, EC 3.4.23.8, EC 3.4.23.9, EC 3.4.23.10, EC 3.4.99.1, EC 3.4.99.15 and EC 3.4.99.25 all created 1972 and incorporated 1978], part incorporated 1992)]

**EC 3.4.23.29**

**Accepted name:** polyporopepsin  
**Reaction:** Milk clotting activity, broad specificity, but fails to cleave Leu\textsuperscript{15}\textsuperscript{-}Tyr or Tyr\textsuperscript{16}\textsuperscript{-}Leu of insulin B chain  
**Other name(s):** Polyporus aspartic proteinase; *Irpex lacteus* aspartic proteinase; *Irpex lacteus* carboxyl proteinase B  
**Comments:** From the basidiomycete *Polyporus tulipiferae* (formerly *Irpex lacteus*). In peptidase family A1 (pepsin A family)  
**References:** [1289, 1291]

[EC 3.4.23.29 created 1992]

**EC 3.4.23.30**

**Accepted name:** pycnoporopepsin  
**Reaction:** Similar to pepsin A, but narrower, cleaving only three bonds in the B chain of insulin: Ala\textsuperscript{14}\textsuperscript{-}Leu, Tyr\textsuperscript{16}\textsuperscript{-}Leu, and Phe\textsuperscript{24}\textsuperscript{-}Phe  
**Other name(s):** proteinase Ia; *Pycnoporus coccineus* aspartic proteinase; Trametes acid proteinase  
**Comments:** From the basidiomycete *Pycnoporus sanguineus*, formerly known as *P. coccineus* and *Trametes sanguinea*. Formerly included in EC 3.4.23.6  
**References:** [2578, 2615, 1070]

[EC 3.4.23.30 created 1992 (EC 3.4.23.6 created 1992 (EC 3.4.23.6 created 1961 as EC 3.4.4.17, transferred 1972 to EC 3.4.23.6, modified 1981 [EC 3.4.23.7, EC 3.4.23.8, EC 3.4.23.9, EC 3.4.23.10, EC 3.4.99.1, EC 3.4.99.15 and EC 3.4.99.25 all created 1972 and incorporated 1978], part incorporated 1992)]

**EC 3.4.23.31**

**Accepted name:** scytalidopepsin A  
**Reaction:** Hydrolysis of proteins with specificity similar to that of pepsin A, but also cleaves Cys(SO\textsubscript{3}H)\textsuperscript{2}\textsuperscript{-}Gly and Leu\textsuperscript{17}\textsuperscript{-}Val in the B chain of insulin  
**Other name(s):** Scytalidium aspartic proteinase A; *Scytalidium lignicolum* aspartic proteinase; *Scytalidium lignicolum* aspartic proteinase A-2; *Scytalidium lignicolum* aspartic proteinase A-I; *Scytalidium lignicolum* aspartic proteinase C; *Scytalidium lignicolum* carboxyl proteinase; *Scytalidium lignicolum* acid proteinase  
**Comments:** Isolated from the imperfect fungus *Scytalidium lignicolum*. Not inhibited by pepstatin-Ac, methyl 2-diazoacetamidohexanoate or 1,2-epoxy-3-(p-nitrophenyl)propane. A related enzyme from the same organism, proteinase C, is also insensitive to these inhibitors and has \( M_r = 406,000 \) [1855]  
**References:** [1850, 1851, 1855]

[EC 3.4.23.31 created 1992]

**EC 3.4.23.32**

**Accepted name:** scytalidopepsin B  
**Reaction:** Hydrolysis of proteins with broad specificity, cleaving Phe\textsuperscript{24}\textsuperscript{-}Phe, but not Leu\textsuperscript{15}\textsuperscript{-}Tyr and Phe\textsuperscript{25}\textsuperscript{-}Tyr in the B chain of insulin  
**Other name(s):** Scytalidium aspartic proteinase B; *Ganoderma lucidum* carboxyl proteinase; *Ganoderma lucidum* aspartic proteinase; *Scytalidium lignicolum* aspartic proteinase B; SLB  

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A second endopeptidase from *Scytalidium lignicolum* (see scytalidopepsin A) that is insensitive to pepstatin and methyl 2-diazoacetamidohexanoate. 1,2-Epoxy-3-(p-nitrophenoxy)propane reacts with Glu$^{53}$, which replaces one of the aspartic residues at the active centre. One of the smallest aspartic endopeptidases active as the monomer, with $M_r$ 22,000. Similarly inhibitor-resistant endopeptidases are found in the basidiomycetes *Lentinus edodes* [2542] and *Ganoderma lucidum* [2543], and in *Polyporus tulipiferae* [1290], a second endopeptidase distinct from polyporopepsin, but these are of typical aspartic endopeptidase size, $M_r$ about 36,000. Type example of peptidase family G1.

References: [2542, 1537, 2543, 1290, 2618]

[EC 3.4.23.32 created 1992]

[3.4.23.33 Transferred entry. xanthomonapepsin. Now EC 3.4.21.101, xanthomonalisin]

[EC 3.4.23.33 created 1992, deleted 2001]

**EC 3.4.23.34**

Accepted name: cathepsin E

Reaction: Similar to cathepsin D, but slightly broader specificity

Other name(s): slow-moving proteinase; erythrocyte membrane aspartic proteinase; SMP; erythrocyte membrane aspartic proteinase; EMAP; non-pan proteinase; cathepsin D-like acid proteinase; cathepsin E-like acid proteinase; cathepsin D-type proteinase

Comments: Found in stomach, spleen, erythrocyte membrane; not lysosomal. Pro-cathepsin E is an 86 kDa disulfide-linked dimer; activation or reduction produces monomer. In peptidase family A1 (pepsin A family)

References: [1377, 2885, 1170, 93]

[EC 3.4.23.34 created 1992]

**EC 3.4.23.35**

Accepted name: barrierpepsin

Reaction: Selective cleavage of -Leu$^6$ Lys- bond in the pheromone α-mating factor

Other name(s): barrier proteinase; Bar proteinase

Comments: A secreted endopeptidase known from baker’s yeast (*Saccharomyces cerevisiae*). In peptidase family A1 (pepsin A family)

References: [1521, 1520]

[EC 3.4.23.35 created 1993]

**EC 3.4.23.36**

Accepted name: signal peptidase II

Reaction: Release of signal peptides from bacterial membrane prolipoproteins including murein prolipoprotein. Hydrolyses -Xaa-Yaa-Zaa-(S,diacylglyceryl)Cys-, in which Xaa is hydrophobic (preferably Leu), and Yaa (Ala or Ser) and Zaa (Gly or Ala) have small, neutral sidechains

Other name(s): premurein-leader peptidase; prolipoprotein signal peptidase; leader peptidase II; premurein leader proteinase; leader peptidase II

Comments: An 18-kDa enzyme present in bacterial inner membranes. Inhibited by pepstatin and the antibiotic globomycin. Type example of peptidase family A8

References: [532, 2915, 2198]

[EC 3.4.23.36 created 1984 as EC 3.4.99.35, transferred 1995 to EC 3.4.23.36]

[3.4.23.37 Transferred entry. pseudomonapepsin. Now EC 3.4.21.100, pseudomonalisin]

[EC 3.4.23.37 created 1995]
EC 3.4.23.38

Accepted name: plasmepsin I
Reaction: Hydrolysis of the -Phe\(^{33}\)-Leu- bond in the \(\alpha\)-chain of hemoglobin, leading to denaturation of the molecule
Other name(s): aspartic hemoglobinase I; PFAPG; malaria aspartic hemoglobinase
Comments: Known from the malaria organism, *Plasmodium*. About 37 kDa. In peptidase family A1 (pepsin A family), closest to cathepsin D and renin in structure. Inhibited by pepstatin. Formerly included in EC 3.4.23.6
References: [838, 719, 830]

[EC 3.4.23.38 created 1995]

EC 3.4.23.39

Accepted name: plasmepsin II
Reaction: Hydrolysis of the bonds linking certain hydrophobic residues in hemoglobin or globin. Also cleaves the small molecule substrates such as Ala-Leu-Glu-Arg-Thr-Phe Phe(NO\(_2\))-Ser-Phe-Pro-Thr [3]
Other name(s): aspartic hemoglobinase II; PFAPD
Comments: Known from the malaria organism, *Plasmodium*. About 37 kDa. In peptidase family A1 (pepsin A family), and is 73% identical in sequence to plasmepsin I. Inhibited by pepstatin. Formerly included in EC 3.4.23.6
References: [474, 830, 1007]

[EC 3.4.23.39 created 1995]

EC 3.4.23.40

Accepted name: phytepsin
Reaction: Prefers hydrophobic residues Phe, Val, Ile, Leu, and Ala at P1 and P1\(^{\prime}\), but also cleaves -Phe\(\rightarrow\)Asp- and -Asp\(\rightarrow\)Asp- bonds in 2S albumin from plant seeds
Comments: Known particularly from barley grain, but present in other plants also. In peptidase family A1 (pepsin A family), but structurally distinct in containing an internal region of about 100 amino acids not generally present in the family
References: [2164, 1235, 72, 1236]

[EC 3.4.23.40 created 1997]

EC 3.4.23.41

Accepted name: yapsin 1
Reaction: Hydrolyses various precursor proteins with Arg or Lys in P1, and commonly Arg or Lys also in P2. The P3 amino acid is usually non-polar, but otherwise additional basic amino acids are favourable in both non-prime and prime positions
Other name(s): yeast aspartic protease 3; Yap3 gene product (*Saccharomyces cerevisiae*)
Comments: In peptidase family A1 of pepsin, and weakly inhibited by pepstatin. Can partially substitute for kexin in a deficient strain of yeast. The homologous product of the Mkc7 gene (*Saccharomyces cerevisiae*) has similar catalytic activity and has been termed yapsin 2 [766]
References: [349, 766, 1900]

[EC 3.4.23.41 created 2000]

EC 3.4.23.42

Accepted name: thermopsin
Reaction: Similar in specificity to pepsin A preferring bulky hydrophobic amino acids in P1 and P1\(^{\prime}\)
Comments: From the thermophilic archeon *Sulfolobus acidocaldarius*. Maximally active at pH 2 and 90 °C. Weakly inhibited by pepstatin but shows no sequence similarity to pepsin. Type example of peptidase family A5.
EC 3.4.23.43
Accepted name: prepilin peptidase
Reaction: Typically cleaves a -Gly-Phe- bond to release an N-terminal, basic peptide of 5-8 residues from type IV prepilin, and then N-methylates the new N-terminal amino group, the methyl donor being S-adenosyl-L-methionine
Comments: Many species of bacteria carry pili on their cell surfaces. These are virulence determinants in pathogenic strains, and are assembled biosynthetically from type IV prepilin subunits. Before assembly, the prepilin molecules require proteolytic processing, which is done by the prepilin peptidase. Prepilin peptidase and its homologues play a central role not only in type IV pilus biogenesis but also in transport of macromolecules across cell membranes. Although both peptide-bond hydrolysis and N-methylation are catalysed by the same molecule, the methylation can be inhibited without affecting peptidase activity, and it is believed that the enzyme has two separate catalytic sites. Type example of peptidase family A24.
References: [1497, 1376]

EC 3.4.23.44
Accepted name: nodavirus endopeptidase
Reaction: Hydrolysis of an asparaginyl bond involved in the maturation of the structural protein of the virus, typically -Asn-Ala- or -Asn-Phe-
Other name(s): Black Beetle virus endopeptidase; Flock House virus endopeptidase
Comments: A single aspartic residue is critical for activity, and inhibition by EDTA indicates that a metal ion is also important. The enzyme is known from several nodaviruses that are pathogens of insects. Type example of peptidase family A6, and structurally related to the tetravirus endopeptidase in family A21, although in that family, the catalytic residue is thought to be Glu.
References: [2924, 1147]

EC 3.4.23.45
Accepted name: memapsin 1
Reaction: Broad endopeptidase specificity. Cleaves Glu-Val-Asn-Leu-Asp-Ala-Glu-Phe in the Swedish variant of Alzheimer’s amyloid precursor protein
Other name(s): β-secretase; β-site Alzheimer’s amyloid precursor protein cleaving enzyme 2 (BACE2); ASP1; Down region aspartic protease
Comments: Can cleave β-amylloid precursor protein to form the amyloidogenic β-peptide that is implicated in the pathology of Alzheimer’s disease, but is not significantly expressed in human brain. In peptidase family A1, but is atypical in containing a C-terminal membrane-spanning domain.
References: [2629]

EC 3.4.23.46
Accepted name: memapsin 2
Reaction: Broad endopeptidase specificity. Cleaves Glu-Val-Asn-Leu-Asp-Ala-Glu-Phe in the Swedish variant of Alzheimer’s amyloid precursor protein
Other name(s): β-secretase; β-site Alzheimer’s amyloid precursor protein cleaving enzyme 1 (BACE1)
Comments: Suggested to be the major “β-secretase” responsible for the cleavage of the β-amyloid precursor protein to form the amyloidogenic β-peptide that is implicated in the pathology of Alzheimer’s disease. In peptidase family A1 but is atypical in containing a C-terminal membrane-spanning domain.

References: [2630, 1032]

[EC 3.4.23.46 created 2003]

EC 3.4.23.47

Accepted name: HIV-2 retropepsin
Reaction: Endopeptidase for which the P1 residue is preferably hydrophobic
Comments: In peptidase family A2. Responsible for the post-translational processing of the human immunodeficiency virus polyprotein.
References: [2590, 379]

[EC 3.4.23.47 created 2003]

EC 3.4.23.48

Accepted name: plasminogen activator Pla
Reaction: Converts human Glu-plasminogen to plasmin by cleaving the Arg^{560}→Val peptide bond that is also hydrolysed by the mammalian u-plasminogen activator and t-plasminogen activator. Also cleaves arginyl bonds in other proteins
Comments: In peptidase family A26. From the bacterium Yersinia pestis that causes plague.
References: [1338]

[EC 3.4.23.48 created 2003]

EC 3.4.23.49

Accepted name: omptin
Reaction: Has a virtual requirement for Arg in the P1 position and a slightly less stringent preference for this residue in the P1’ position, which can also contain Lys, Gly or Val.
Other name(s): protease VII; protease A; gene ompT proteins; ompT protease; protein a; Pla; protease VII; protease A; OmpT
Comments: A product of the ompT gene of Escherichia coli, and associated with the outer membrane. Omptin shows a preference for cleavage between consecutive basic amino acids, but is capable of cleavage when P1’ is a non-basic residue [2679, 1611]. Belongs in peptidase family A26.
References: [878, 2442, 920, 511, 2679, 1323, 1611]

[EC 3.4.23.49 created 1993 as EC 3.4.21.87, transferred 2006 to EC 3.4.23.49]

EC 3.4.23.50

Accepted name: human endogenous retrovirus K endopeptidase
Reaction: Processing at the authentic HIV-1 PR recognition site and release of the mature p17 matrix and the p24 capsid protein, as a result of the cleavage of the -SQNY→PIVQ- cleavage site.
Other name(s): human endogenous retrovirus K10 endopeptidase; endogenous retrovirus HERV-K10 putative protease; human endogenous retrovirus K retropepsin; HERV K10 endopeptidase; HERV K10 retropepsin; HERV-K PR; HERV-K protease; HERV-K113 protease; human endogenous retrovirus K113 protease; human retrovirus K10 retropepsin
Comments: In peptidase family A2.
References: [2587]

[EC 3.4.23.50 created 2009]
EC 3.4.23.51

**Accepted name:** HycI peptidase  
**Reaction:** This enzyme specifically removes a 32-amino acid peptide from the C-terminus of the precursor of the large subunit of hydrogenase 3 in *Escherichia coli* by cleavage at the C-terminal side of Arg537.  
**Other name(s):** HycI; HycE processing protein  
**Comments:** The reaction requires nickel to be bound to the precursor of the large subunit of hydrogenase 3. The endopeptidase uses the metal in the large subunit of [NiFe]-hydrogenases as a recognition motif [2546]. In peptidase family A31.  
**References:** [2546, 2856]

[EC 3.4.23.51 created 2009]

**EC 3.4.24 Metalloendopeptidases**

EC 3.4.24.1  
**Accepted name:** atrolysin A  
**Reaction:** Cleavage of Asn3-Gln, His5-Leu, His10-Leu, Ala14-Leu and Tyr16-Leu in insulin B chain; removes C-terminal Leu from small peptides  
**Other name(s):** *Crotalus atrox* metalloendopeptidase a; hemorrhagic toxin a; *Crotalus atrox* α-proteinase; *Crotalus atrox* proteinase; bothropasin  
**Comments:** A hemorrhagic endopeptidase of 68 kDa, one of six hemorrhagic toxins in the venom of western diamondback rattlesnake. The 60 kDa hemorrhagic toxin 1 of *Crotalus ruber ruber* shows identical specificity [1702]. In peptidase family M12 (astacin family). Related metalloendopeptidases from rattlesnake venoms are EC 3.4.24.41 (atrolysin B), EC 3.4.24.42 (atrolysin C), EC 3.4.24.43 (atroxase), EC 3.4.24.44 (atrolysin E), EC 3.4.24.45 (atrolysin F), EC 3.4.24.46 (adamalysin), EC 3.4.24.47 (horrilysin), and EC 3.4.24.48 (ruberyllysin)  
**References:** [203, 1702, 202, 201]

[EC 3.4.24.1 created 1972, modified 1986]

[3.4.24.2 Deleted entry. *Sepia* proteinase]  

[EC 3.4.24.2 created 1972, deleted 1992]

EC 3.4.24.3  
**Accepted name:** microbial collagenase  
**Reaction:** Digestion of native collagen in the triple helical region at Gly bonds. With synthetic peptides, a preference is shown for Gly at P3 and P1', Pro and Ala at P2 and P2', and hydroxyproline, Ala or Arg at P3'  
**Other name(s):** *Clostridium histolyticum* collagenase; clostridiopeptidase A; collagenase A; collagenase I; *Achromobacter* iophagus collagenase; collagenase; aspergillopeptidase C; nucleolysin; azocollase; metallocollagenase; soycollagestin; *Clostridium histolyticum* proteinase A; clostridiopeptidase II; MMP-8; clostridiopeptidase I; collagen peptidase; collagen protease; collagenase MMP-1; metalloproteinase-1; kollaza; matrix metalloproteinase-1; MMP-1; matrix metalloproteinase-8; matrix metalloproteinase-18; interstitial collagenase  
**Comments:** Six species of metalloendopeptidase acting on native collagen can be isolated from the medium of *Clostridium histolyticum*. Class I has forms α (68 kDa), β (115 kDa) and γ (79 kDa); class II has δ (100 kDa), ε (110 kDa) and ζ (125 kDa). The two classes are immunologically crossreactive, but have significantly different sequences, and different specificities such that their actions on collagen are complementary. The enzymes also act as peptidyl-tripeptidases. Variants of the enzyme have been purified from *Bacillus cereus* [1540], *Empedobacter collagenolyticum* [1369], *Pseudomonas marinoglutinosa* [917], and species of *Vibrio*, *Vibrio* B-30 (ATCC 21250) [1640] and *V. alginolyticus* (previously *Achromobacter* iophagus) [970, 2581]. Also known from *Streptomyces* sp. [627]. The *Vibrio* enzyme is the type example of peptidase family M9.  
**References:** [917, 1640, 970, 1369, 237, 238, 2750, 2581, 627, 1540]
[EC 3.4.24.3 created 1961 as EC 3.4.4.19, transferred 1972 to EC 3.4.24.3 (EC 3.4.24.8 created 1978, incorporated 1992, EC 3.4.99.5 created 1972, incorporated 1978)]

[3.4.24.4 Transferred entry. now EC 3.4.24.40 serralysin]
[EC 3.4.24.4 created 1972 [EC 3.4.99.13 and EC 3.4.99.22 both created 1972, incorporated 1978], deleted 1992]

[3.4.24.5 Deleted entry. lens neutral proteinase. Now included with EC 3.4.22.53 (calpain-2) and EC 3.4.25.1 (proteasome endopeptidase complex)]
[EC 3.4.24.5 created 1978, deleted 1989]

**EC 3.4.24.6**

**Accepted name:** leucylsine  
**Reaction:** Cleavage of Phe¹ → Val, His⁵ → Leu, Ala¹⁴ → Leu, Gly²⁰ → Glu, Gly²³ → Phe and Phe²⁴ → Phe bonds in insulin B chain as well as N-blocked dipeptides  
**Other name(s):** Leucostoma neutral proteinase; Leucostoma peptidase A  
**Comments:** From the venom of the western cottonmouth moccasin snake (Agkistrodon piscivorus leucostoma).  
**References:** [2709, 2400]

[EC 3.4.24.6 created 1978]

**EC 3.4.24.7**

**Accepted name:** interstitial collagenase  
**Reaction:** Cleavage of the triple helix of collagen at about three-quarters of the length of the molecule from the N-terminus, at Gly⁷⁷⁵ → Ile in the α(1)(I) chain. Cleaves synthetic substrates and α-macroglobulins at bonds where P¹′ is a hydrophobic residue  
**Other name(s):** vertebrate collagenase; matrix metalloproteinase 1  
**Comments:** The enzyme takes its name from substrates of the interstitial collagen group - types I, II and III, all of which are cleaved in the helical domain. However, α-macroglobulins are cleaved much more rapidly. The enzyme is widely distributed in vertebrate animals. Type example of peptidase family M10  
**References:** [839, 196, 684, 2393]

[EC 3.4.24.7 created 1978]

[3.4.24.8 Transferred entry. Achromobacter iophagus collagenase. Now EC 3.4.24.3, microbial collagenase]
[EC 3.4.24.8 created 1978, deleted 1992]

[3.4.24.9 Deleted entry. Trichophyton schoenleinii collagenase]
[EC 3.4.24.9 created 1978, deleted 1992]

[3.4.24.10 Deleted entry. Trichophyton mentagrophytes keratinase]
[EC 3.4.24.10 created 1972 as EC 3.4.99.12, transferred 1978 to EC 3.4.24.10, deleted 1992]

**EC 3.4.24.11**

**Accepted name:** neprilysin  
**Reaction:** Preferential cleavage of polypeptides between hydrophobic residues, particularly with Phe or Tyr at P¹′  
**Other name(s):** neutral endopeptidase; endopeptidase 24.11; kidney-brush-border neutral peptidase; enkephalinase (misleading); endopeptidase-2; CALLA (common acute lymphoblastic leukemia-associated) antigens; CALLA antigen; endopeptidase; membrane metalloendopeptidase; kidney-brush-border neutral endopeptidase; kidney-brush-border neutral proteinase; endopeptidase-2; CALLA glycoprotein; CALLA; common acute lymphoblastic leukemia antigen; CALLA glycoproteins; common acute lymphoblastic leukemia-associated antigens; neutral metalloendopeptidase; membrane metalloendopeptidase; NEP; neutral endopeptidase 24.11; CD10; neutral endopeptidase; acute lymphoblastic leukemia antigen

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**Comments:** A membrane-bound glycoprotein widely distributed in animal tissues. Inhibited by phosphoramidon and thiorphan. Common acute lymphoblastic leukemia antigen (CALLA). Type example of peptidase family M13

**References:** [1589, 1544, 1425, 635]

**EC 3.4.24.12**

**Accepted name:** envelysin  
**Reaction:** Hydrolysis of proteins of the fertilization envelope and dimethylcasein  
**Other name(s):** sea-urchin-hatching proteinase; hatching enzyme; chorionase; chorion-digesting proteinase; chymostrypsin; sea urchin embryo hatching enzyme  
**Comments:** A glycoprotein from various members of the class Echinoidea. Extracellular enzyme requiring Ca$^{2+}$. In peptidase family M10 (interstitial collagenase family)  
**References:** [142, 1423, 1424, 1826]

**EC 3.4.24.13**

**Accepted name:** IgA-specific metalloendopeptidase  
**Reaction:** Cleavage of Pro-Thr bond in the hinge region of the heavy chain of human IgA  
**Other name(s):** immunoglobulin A$_1$ protease; IgA protease; IgA1-specific proteinase; IgA$_1$ protease; IgA$_1$ proteinase  
**Comments:** A 190 kDa enzyme found in several pathogenic species of Streptococcus such as sanguis and pneumoniae. Type example of peptidase family M26. There is also an IgA-specific prolyl endopeptidase of the serine-type (see EC 3.4.21.72, IgA-specific serine endopeptidase)  
**References:** [1313, 817, 816]

**EC 3.4.24.14**

**Accepted name:** procollagen N-endopeptidase  
**Reaction:** Cleaves the N-propeptide of collagen chain $\alpha$1(I) at Pro-Gln and of $\alpha$1(II) and $\alpha$2(I) at Ala-Gln  
**Other name(s):** procollagen N-terminal peptidase; procollagen aminopeptidase; aminopprocollagen peptidase; aminoterminal procollagen peptidase; procollagen aminoterminal protease; procollagen N-terminal protease; type II procollagen N-proteinase; type III procollagen  
**Comments:** Removes the propeptides of type I and II collagens prior to fibril assembly. Does not act on type III collagen. In peptidase family M12 (astacin family)  
**References:** [1297, 1025]

**EC 3.4.24.15**

**Accepted name:** thimet oligopeptidase  
**Reaction:** Preferential cleavage of bonds with hydrophobic residues at P1, P2 and P3′ and a small residue at P1′ in substrates of 5-15 residues  
**Other name(s):** Pz-peptidase; soluble metalloendopeptidase; endo-oligopeptidase A; tissue-endopeptidase degrading collagenase-synthetic-substrate  
**Comments:** Thiol compounds activate at low concentrations. Type example of peptidase family M3.  
**References:** [406, 1907, 139, 1977, 2563]

[EC 3.4.24.15 created 1984 (EC 3.4.22.19 created 1989 and EC 3.4.99.31 created 1978 both incorporated 1992)]
EC 3.4.24.16

Accepted name: neurolysin

Reaction: Preferential cleavage in neurotensin: Pro\(^{10}\)→Tyr

Other name(s): neurotensin endopeptidase; endopeptidase 24.16; endo-oligopeptidase B (proline-endopeptidase)

Comments: No absolute requirement for a prolyl bond: the enzyme acts on some peptides, such as dynorphin 1-8, that do not contain proline, and does not act on some others that do. In peptidase family M3 (thimet oligopeptidase family)

References: [370, 124, 369]

EC 3.4.24.17

Accepted name: stromelysin 1

Reaction: Preferential cleavage where P1′, P2′ and P3′ are hydrophobic residues

Other name(s): matrix metalloproteinase 3; proteoglycanase; collagenase activating protein; procollagenase activator; transin; MMP-3; neutral proteoglycanase; stromelysin; collagen-activating protein


References: [392, 1891, 554, 625]

EC 3.4.24.18

Accepted name: meprin A

Reaction: Hydrolysis of protein and peptide substrates preferentially on carboxyl side of hydrophobic residues

Other name(s): endopeptidase-2; meprin-a; meprin; N-benzoyl-L-tyrosyl-p-aminobenzoic acid hydrolase; PABA-peptide hydrolase; PPH

Comments: A membrane-bound metalloendopeptidase of rat and mouse kidney and intestinal brush borders, and salivary ducts. Differences from neprilysin (EC 3.4.24.11 (astacin family). Formerly included in EC 3.4.24.11

References: [188, 308, 2420, 2421, 130]

EC 3.4.24.19

Accepted name: procollagen C-endopeptidase

Reaction: Cleavage of the C-terminal propeptide at Ala→Asp in type I and II procollagens and at Arg→Asp in type III

Other name(s): procollagen C-terminal proteinase; carboxyprocollagen peptidase; procollagen C-terminal peptidase; procollagen C-protease; procollagen C-terminal proteinase; procollagen carboxypeptidase; procolla-gen carboxy-terminal proteinase; procollagen peptidase

Comments: A 100 kDa endopeptidase the activity of which is increased by Ca\(^{2+}\) and by an enhancer glycoprotein. In peptidase family M12 (astacin family)

References: [1026, 1238]

EC 3.4.24.20

Accepted name: peptidyl-Lys metalloendopeptidase

Reaction: Preferential cleavage in proteins: -Xaa→Lys- (in which Xaa may be Pro)

Other name(s): Armillaria mellea neutral proteinase; peptidyllysine metalloproteinase

Comments: From the honey fungus Armillaria mellea. In peptidase family M35 (deuterolysin family)

References: [2169, 1435]
| EC 3.4.24.21 | **Accepted name:** astacin  
**Reaction:** Hydrolysis of peptide bonds in substrates containing five or more amino acids, preferentially with Ala in P1', and Pro in P2'  
**Other name(s):** Astacus proteinase; crayfish small-molecule proteinase  
**Comments:** A 22.6 kDa digestive endopeptidase from the cardia of the crayfish Astacus fluviatilis. Type example of peptidase family M12.  
**References:** [1324, 2565, 2432, 2431] |
| EC 3.4.24.22 | **Accepted name:** stromelysin 2  
**Reaction:** Similar to stromelysin 1, but action on collagen types III, IV and V is weak  
**Other name(s):** matrix metalloproteinase 10; transin 2; proteoglycanase 2  
**Comments:** In peptidase family M10 (interstitial collagenase family). Digests gelatin types I, III, IV, V, fibronectin and proteoglycan  
**References:** [260, 1728, 1803] |
| EC 3.4.24.23 | **Accepted name:** matrilysin  
**Reaction:** Cleavage of Ala\textsuperscript{14}Leu and Tyr\textsuperscript{16}Leu in B chain of insulin. No action on collagen types I, II, IV, V. Cleaves gelatin chain α\textsubscript{2}(I)  
\; α\textsubscript{1}(I)  
**Other name(s):** matrin; uterine metalloendopeptidase; matrix metalloproteinase 7; putative (or punctuated) metalloproteinase-1; matrix metalloproteinase pump 1; MMP 7; PUMP-1 proteinase; PUMP; metalloproteinase pump-1; putative metalloproteinase; MMP  
**Comments:** Found in rat uterus; at 19 kDa, the smallest member of peptidase family M10 (interstitial collagenase family). Similar in specificity to stromelysin, but more active on azocoll  
**References:** [1728, 2818, 2028, 1681] |
| EC 3.4.24.24 | **Accepted name:** gelatinase A  
**Reaction:** Cleavage of gelatin type I and collagen types IV, V, VII, X. Cleaves the collagen-like sequence Pro-Gln-Gly-Ile-Ala-Gly-Gln  
**Other name(s):** 72-kDa gelatinase; matrix metalloproteinase 2; type IV collagenase; 3/4 collagenase (Obsolete); matrix metalloproteinase 5 (Obsolete); 72 kDa gelatinase type A; collagenase IV; collagenase type IV; MMP 2; type IV collagen metalloproteinase; type IV collagenase/gelatinase; matrix metalloproteinase 2  
**Comments:** A secreted endopeptidase in peptidase family M10 (interstitial collagenase family), but possessing an additional fibronectin-like domain  
**References:** [1740, 421, 1892] |
| EC 3.4.24.25 | **Accepted name:** vibriolysin |
Reaction: Preferential cleavage of bonds with bulky hydrophobic groups in P2 and P1'. Phe at P1' is the most favoured residue, which distinguished this enzyme from thermolysin

Other name(s): *Aeromonas proteolytica* neutral proteinase; aeromonolysin

Comments: Thermostable enzyme from *Vibrio proteolyticus* (formerly *Aeromonas proteolytica*). Specificity related to, but distinct from, those of thermolysin and bacillolysin [1030]. A zinc metallopeptidase in family M4 (thermolysin family). Formerly included in EC 3.4.24.4

References: [1030, 2802, 156, 2801, 484]

EC 3.4.24.26

Accepted name: pseudolysin

Reaction: Hydrolysis of proteins including elastin, collagen types III and IV, fibronectin and immunoglobulin A, generally with bulky hydrophobic group at P1'. Insulin B chain cleavage pattern identical to that of thermolysin, but specificity differs in other respects

Other name(s): *Pseudomonas* elastase; *Pseudomonas aeruginosa* neutral metalloproteinase

Comments: In peptidase family M4 (thermolysin family). From the pathogenic bacteria *Pseudomonas aeruginosa* and *Legionella pneumophila*, and causes tissue damage.

References: [1707, 1816, 581, 187, 209]

EC 3.4.24.27

Accepted name: thermolysin

Reaction: Preferential cleavage: Leu → Phe

Other name(s): *Bacillus* thermoproteolyticus neutral proteinase; thermoase; thermoase Y10; TLN

Comments: A thermostable extracellular metalloendopeptidase containing four calcium ions. Enzymes that may be species variants of thermolysin are reported from *Micrococcus caseolyticus* [524] and *Aspergillus oryzae* [1706]. Type example of peptidase family M4. Closely related but distinct enzymes are aeromonolysin, pseudolysin, bacillolysin, aureolysin and mycolysin

References: [1885, 1709, 1386, 524, 1706, 2564, 1599]

EC 3.4.24.28

Accepted name: bacillolysin

Reaction: Similar, but not identical, to that of thermolysin

Other name(s): *Bacillus* metalloendopeptidase; *Bacillus subtilis* neutral proteinase; anilozyme P 10; *Bacillus* metalloproteinase; *Bacillus* neutral proteinase; megariteriopeptidase

Comments: Variants of this enzyme have been found in species of *Bacillus* including *B. subtilis* [1709, 2858], *B. amyloliquefaciens* [2683], *B. megaterium* (megetteroppeptidase, [1663]), *B. mesentericus* [2433], *B. cereus* [3,8,9] and *B. stearothermophilus* [2479]. In peptidase family M4 (thermolysin family). Formerly included in EC 3.4.24.4

References: [1709, 1663, 673, 1030, 2683, 2858, 2858, 2479, 2319, 1950, 2433]

EC 3.4.24.29

Accepted name: aureolysin

Reaction: Cleavage of insulin B chain with specificity similar to that of thermolysin, preferring hydrophobic P1' residue. Activates the glutamyl endopeptidase (EC 3.4.21.19) of *Staphylococcus aureus*

Other name(s): *Staphylococcus aureus* neutral proteinase; *Staphylococcus aureus* neutral protease

Comments: A metalloenzyme from *S. aureus* earlier confused with staphylokinase (a non-enzymatic activator of plasminogen).
References: [71, 2178, 577, 2010]

[EC 3.4.24.29 created 1972 as EC 3.4.24.4, part transferred 1992 to EC 3.4.24.29]

EC 3.4.24.30
Accepted name: coccolysin
Reaction: Preferential cleavage: Leu, Phe, Tyr, Ala
Other name(s): Streptococcus thermophilus intracellular proteinase; EM 19000
Comments: A 30 kDa endopeptidase found intracellularly in S. thermophilus [525] and S. diacetilactis [526] and in the medium of S. faecalis [2367, 1541]. In peptidase family M4 (thermolysin family). Formerly included in EC 3.4.24.4
References: [525, 526, 2367, 1541]

[EC 3.4.24.30 created 1972 as EC 3.4.24.4, part transferred 1992 to EC 3.4.24.30]

EC 3.4.24.31
Accepted name: mycolysin
Reaction: Preferential cleavage of bonds with hydrophobic residues in P1′
Other name(s): pronase component; Streptomyces griseus neutral proteinase; actinase E; SGNPI
Comments: From Streptomyces griseus, S. naraensis, and S. cacaoi. Specificity similar to that of thermolysin, but much more sensitive to inhibition by mercaptoacetyl-Phe-Leu. Little structural similarity to other bacterial metalloendopeptidases. Type example of peptidase family M5. Formerly included in EC 3.4.24.4
References: [1709, 1011, 225, 360]

[EC 3.4.24.31 created 1972 as EC 3.4.24.4, part transferred 1992 to EC 3.4.24.31]

EC 3.4.24.32
Accepted name: β-lytic metalloendopeptidase
Reaction: Cleavage of N-acetylmuramoyl-Ala, and of the insulin B chain at Gly-Phe Val Val Cya
Other name(s): Myxobacter β-lytic proteinase; achromopeptidase component; β-lytic metalloproteinase; β-lytic proteinase; Myxobacterium sorangium β-lytic proteinase; Myxobacter β-lytic proteinase
Comments: From Achromobacter lyticus and Lysobacter enzymogenes. Digests bacterial cell walls. Type example of peptidase family M23.
References: [2787, 2786, 1440]

[EC 3.4.24.32 created 1972 as EC 3.4.24.4, part transferred 1992 to EC 3.4.24.32]

EC 3.4.24.33
Accepted name: peptidyl-Asp metalloendopeptidase
Reaction: Cleavage of Xaa-Asp, Xaa-Glu and Xaa-cysteic acid bonds
Other name(s): endoproteinase Asp-N; peptidyl-Asp metalloproteinase
Comments: A metalloenzyme isolated from Pseudomonas fragi. Useful in protein sequencing applications because of its limited specificity. In peptidase family M72.
References: [2007, 579, 1091]

[EC 3.4.24.33 created 1992]

EC 3.4.24.34
Accepted name: neutrophil collagenase
Reaction: Cleavage of interstitial collagens in the triple helical domain. Unlike EC 3.4.24.7, interstitial collaegenase, this enzyme cleaves type III collagen more slowly than type I
**Other name(s):** matrix metalloproteinase 8; PMNL collagenase; MMP-8  
**Comments:** Similar to interstitial collagenase in specificity, but the product of a different gene and highly glycosylated. Stored in the specific granules of neutrophil leukocytes. In peptidase family M10 (interstitial collagenase family). Formerly included in EC 3.4.24.7  
**References:** [946, 947, 1285]

[EC 3.4.24.34 created 1992]

**EC 3.4.24.35**  
**Accepted name:** gelatinase B  
**Reaction:** Cleavage of gelatin types I and V and collagen types IV and V  
**Other name(s):** 92-kDa gelatinase; matrix metalloproteinase 9; type V collagenase; 92-kDa type IV collagenase; macrophage gelatinase; 95 kDa type IV collagenase/gelatinase; collagenase IV; collagenase type IV; gelatinase MMP 9; MMP 9; matrix metalloproteinase 9; type IV collagen metalloproteinase  
**Comments:** Similar to gelatinase A, but possesses a further domain. In peptidase family M10 (interstitial collagenase family)  
**References:** [1004, 2798, 1535]

[EC 3.4.24.35 created 1992]

**EC 3.4.24.36**  
**Accepted name:** leishmanolysin  
**Reaction:** Preference for hydrophobic residues at P1 and P1′ and basic residues at P2′ and P3′. A model nonapeptide is cleaved at -Ala-Tyr-Leu-Lys-Lys-  
**Other name(s):** promastigote surface endopeptidase; glycoprotein gp63; Leishmania metalloproteinase; surface acid proteinase; promastigote surface protease  
**Comments:** A membrane-bound glycoprotein found on the promastigote of various species of Leishmania protozoans. Contains consensus sequence for a zinc-binding site; Z-Tyr-Leu-NHOH is a strong inhibitor. The enzyme can activate its proenzyme by cleavage of the Val[106]Val bond. An acid pH optimum is found with certain protein substrates. Type example of peptidase family M8  
**References:** [314, 248, 368, 249]

[EC 3.4.24.36 created 1992]

**EC 3.4.24.37**  
**Accepted name:** saccharolysin  
**Reaction:** Cleavage of Pro-Phe and Ala-Ala bonds  
**Other name(s):** proteinase yscD; yeast cysteine proteinase D (Misleading); Saccharomyces cerevisiae proteinase yscD  
**Comments:** An 83 kDa cytoplasmic thiol-dependent metalloendopeptidase from Saccharomyces cerevisiae. In peptidase family M3 (thimet oligopeptidase family).  
**References:** [10, 777]

[EC 3.4.24.37 created 1989 as EC 3.4.22.22, transferred 1992 to EC 3.4.24.37]

**EC 3.4.24.38**  
**Accepted name:** gametolysin  
**Reaction:** Cleavage of the proline- and hydroxyproline-rich proteins of the Chlamydomonas cell wall; also cleaves azocasein, gelatin and Leu-Trp-Met-Arg-Phe-Ala  
**Other name(s):** autolysin, Chlamydomonas cell wall degrading protease; lysin; Chlamydomonas reinhardtii metalloproteinase; gamete lytic enzyme; gamete autolysin  
**Comments:** A glycoprotein found in the periplasmic space of Chlamydomonas reinhardtii gametes in a 62 kDa inactive form; decreased to 60 kDa upon activation. A zinc enzyme, inhibited by phosphoramidon, but also thiol activated. Type example of peptidase family M11  
**References:** [1120, 299, 1590]

205
EC 3.4.24.39
Accepted name: deuterolysin
Reaction: Cleavage of the proline- and hydroxyproline-rich proteins of the Chlamydomonas cell wall; also cleaves azocasein, gelatin and Leu-Trp-Met-Arg-Phe-Ala
Other name(s): Penicillium roqueforti protease II; microbial neutral proteinase II; acid metalloproteinase; neutral proteinase II; Penicillium roqueforti metalloproteinase
Comments: Proteolytic activity found in Penicillium roqueforti [874], P. caseicolum [874], Aspergillus sojae [2276] and A. oryzae [1762, 2656]. Optimum pH of 5 for digesting various proteins. Strong action on protamine and histones. Insensitive to phosphoramidon. About 20 kDa. A distinct Aspergillus sojae endopeptidase is larger and has a neutral pH optimum. Type example of peptidase family M35. Formerly included in EC 3.4.24.4
References: [1762, 873, 2276, 874, 2656]

[EC 3.4.24.39 created 1972 as EC 3.4.24.4, part transferred 1992 to EC 3.4.24.39]

EC 3.4.24.40
Accepted name: serralysin
Reaction: Preferential cleavage of bonds with hydrophobic residues in P1'
Other name(s): Pseudomonas aeruginosa alkaline proteinase; Escherichia freundii proteinase; Serratia marcescens extracellular proteinase; Serratia marcescens metalloproteinase; Pseudomonas aeruginosa alk. protease; Serratia marcescens metalloprotease
Comments: A 50 kDa extracellular endopeptidase from Pseudomonas aeruginosa [1,2,6], Escherichia freundii [1768], Serratia marcescens [4,5,6] and Erwinia chrysanthemi [469]. There is broad specificity in cleavage of the insulin B chain, with some species variations. The pH optimum for digesting various proteins is about 9 - 10. In peptidase family M10 (interstitial collagenase family). Formerly included in EC 3.4.24.4
References: [1709, 1710, 1768, 505, 558, 1766, 469, 1896]

[EC 3.4.24.40 created 1972 as EC 3.4.24.4, part transferred 1992 to EC 3.4.24.40]

EC 3.4.24.41
Accepted name: atrolysin B
Reaction: Cleavage of His5-Leu, His10-Leu, Ala14-Leu, Tyr16-Leu and Gly23-Phe of insulin B chain; identical to the cleavage of insulin B chain by atrolysin C. Also cleaves Ser bonds in glucagon
Other name(s): Crotalus atrox metalloendopeptidase b; hemorrhagic toxin b; Ht-b
Comments: From the venom of the western diamondback rattlesnake (Crotalus atrox). In peptidase family M12 (astacin family)
References: [203, 202]

[EC 3.4.24.41 created 1992]

EC 3.4.24.42
Accepted name: atrolysin C
Reaction: Cleavage of His5-Leu, His10-Leu, Ala14-Leu, Tyr16-Leu and Gly23-Phe bonds in B chain of insulin. With small molecule substrates prefers hydrophobic residue at P2' and small residue such as Ala, Gly at P1
Other name(s): Crotalus atrox metalloendopeptidase c; hemorrhagic toxin c and d
Comments: A 24 kDa hemorrhagic endopeptidase from the venom of the western diamondback rattlesnake (Crotalus atrox) that digests type IV collagen, and exists as two forms, c and d. Phosphoramidon inhibits in the 0.1 mM range. In peptidase family M12 (astacin family). Hemorrhagic toxin-2 of C. ruber ruber has the same Mr and specificity and is a homologue [1702, 2506].
References: [203, 716, 200, 1702, 2286, 2506]

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EC 3.4.24.43
Accepted name: atroxase
Reaction: Cleavage of His⁵→Leu, Ser⁹→His, His¹⁰→Leu, Ala¹⁴→Leu and Tyr¹⁶→Leu of insulin B chain
Comments: A nonhemorrhagic endopeptidase from the venom of the western diamondback rattlesnake (Crotalus atrox) that cleaves fibrinogen. In peptidase family M12 (astacin family)
References: [2806]

EC 3.4.24.44
Accepted name: atrolysin E
Reaction: Cleavage of Asn³→Gln, Ser⁹→His and Ala¹⁴→Leu bonds in insulin B chain and Tyr¹⁴→Gln and Thr⁹→Ser in A chain. Cleaves type IV collagen at Ala⁷³→Gln in α1(IV) and at Gly⁷→Leu in α2(IV)
Other name(s): Crotalus atrox metalloendopeptidase e; hemorrhagic toxin e
Comments: A 25.7 kDa hemorrhagic endopeptidase from the venom of the western diamondback rattlesnake (Crotalus atrox) that digests basement membrane components, including the triple helix of type IV collagen. Such action is believed to contribute to the hemorrhagic property by weakening capillary walls. In peptidase family M12 (astacin family)
References: [203, 199, 121]

EC 3.4.24.45
Accepted name: atrolysin F
Reaction: Cleavage of Val²→Asn, Gln⁴→His, Leu⁶→Cys, His¹⁰→Leu, Ala¹⁴→Leu and Tyr¹⁶→Leu bonds in insulin B chain
Other name(s): Crotalus atrox metalloendopeptidase; hemorrhagic toxin f; Crotalus atrox metalloendopeptidase f
Comments: A 64 kDa hemorrhagic endopeptidase from the venom of the western diamondback rattlesnake (Crotalus atrox) that digests the γ chain of fibrinogen. Immunologically distinct from EC 3.4.24.1, atrolysin A.
References: [1807]

EC 3.4.24.46
Accepted name: adamalysin
Reaction: Cleavage of Phe¹→Val, His⁵→Leu, His¹⁰→Leu, Ala¹⁴→Leu, Leu¹⁵→Tyr, and Tyr¹⁶→Leu of insulin B chain
Other name(s): Crotalus adamanteus metalloendopeptidase; proteinase I and II; Crotalus adamanteus venom proteinase II; adamalysin II
Comments: From the venom of the eastern diamondback rattlesnake (Crotalus adamanteus). Two isoenzymes of approx. 24 kDa that inactivate α₁-proteinase inhibitor by a single cleavage. In peptidase family M12 (astacin family)
References: [1355]

EC 3.4.24.47
Accepted name: horrilysin
**Reaction:** Cleavage of only the single bond Ala\(^{14}\) → Leu in the insulin B chain, Ser\(^{12}\) → Leu in the A chain, and Ile → Gly, Pro → Ala, and Ser → Trp in melittin

**Other name(s):** Crotalus horridus metalloendopeptidase; hemorrhagic proteinase IV; Crotalus horridus horridus venom hemorrhagic proteinase

**Comments:** A 56 kDa hemorrhagic endopeptidase from the venom of the timber rattlesnake (*Crotalus horridus horridus*) that cleaves basement membrane, hide powder and fibrinogen.

**References:** [409, 410]

[EC 3.4.24.47 created 1992]

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**EC 3.4.24.48**

**Accepted name:** ruberylisin

**Reaction:** Cleavage of His\(^{10}\) → Leu, Ala\(^{14}\) → Leu, Tyr\(^{16}\) → Leu and Gly\(^{23}\) → Phe bonds in the B chain of insulin; His → Pro, Pro → Phe, and Trp → Ser of angiotensin I; and Gly → Phe of Met enkephalin

**Other name(s):** *Crotalus ruber* metalloendopeptidase II; hemorrhagic toxin II

**Comments:** A 25 kDa hemorrhagic endopeptidase from the venom of the red rattlesnake (*Crotalus ruber ruber*) that cleaves fibrinogen. In peptidase family M12 (astacin family)

**References:** [1702, 2506]

[EC 3.4.24.48 created 1992]

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**EC 3.4.24.49**

**Accepted name:** bothropasin

**Reaction:** Cleavage of His\(^{5}\) → Leu, His\(^{10}\) → Leu, Ala\(^{14}\) → Leu, Tyr\(^{16}\) → Leu and Phe\(^{24}\) → Phe in insulin B chain

**Other name(s):** *Bothrops jararaca* venom metalloproteinase

**Comments:** Caseinolytic endopeptidase of jararaca snake (*Bothrops jararaca*) venom; 48 kDa. In peptidase family M12

**References:** [1552]

[EC 3.4.24.49 created 1992]

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**EC 3.4.24.50**

**Accepted name:** bothrolysin

**Reaction:** Cleavage of Gln\(^{4}\) → His, Ser\(^{9}\) → His and Ala\(^{14}\) → Leu of insulin B chain and Pro → Phe of angiotensin I

**Other name(s):** Bothrops metalloendopeptidase J; J protease

**Comments:** A 22.5 kDa endopeptidase from the venom of the jararaca snake (*Bothrops jararaca*), insensitive to phosphoramidon at 0.5 mM. In peptidase family M12 (astacin family)

**References:** [2524]

[EC 3.4.24.50 created 1992]

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**EC 3.4.24.51**

**Accepted name:** ophiolysin

**Reaction:** Cleavage of Asn\(^{3}\) → Gln, Gln\(^{4}\) → His, His\(^{10}\) → Leu, Ala\(^{14}\) → Leu, and Tyr\(^{16}\) → Leu in insulin B chain

**Other name(s):** Ophiophagus metalloendopeptidase

**Comments:** A 70 kDa endopeptidase from the venom of the king cobra (*Ophiophagus hannah*)

**References:** [2846]

[EC 3.4.24.51 created 1992]

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**EC 3.4.24.52**

208
Accepted name: trimerelysin I
Reaction: Cleavage of only two bonds His$^{10}$Leu and Ala$^{14}$Leu in the insulin B chain
Other name(s): Trimeresurus metalloendopeptidase I; hemorrhagic proteinase HR1A; hemorrhagic metalloproteinase HR1A
Comments: A 60 kDa hemorrhagic endopeptidase of pI 4.4 from the venom of the habu snake (*Trimeresurus flavoviridis*). In peptidase family M12 (astacin family)
References: [1904, 2847, 2505]

[EC 3.4.24.52 created 1992]

EC 3.4.24.53
Accepted name: trimerelysin II
Reaction: Cleavage of Asn$^{3}$Gln, His$^{10}$Leu and Ala$^{14}$Leu in the insulin B chain, and the bond Z-Gly-Pro-Leu-Gly-Pro in a small molecule substrate of microbial collagenase
Other name(s): Trimeresurus metalloendopeptidase II; proteinase H$_2$; H$_2$-proteinase
Comments: A 24 kDa nonhemorrhagic endopeptidase from the venom of the habu snake (*Trimeresurus flavoviridis*). In peptidase family M12 (astacin family)
References: [2490, 2503]

[EC 3.4.24.53 created 1992]

EC 3.4.24.54
Accepted name: mucrolysin
Reaction: Cleavage of Ser$^{9}$His, His$^{10}$Leu, Ala$^{14}$Leu, Leu$^{15}$Tyr and Tyr$^{16}$Leu bonds in insulin B chain
Other name(s): Trimeresurus metalloendopeptidase A; mucrotoxin A
Comments: A 94 kDa hemorrhagic and fibrinogenolytic endopeptidase from the Chinese habu snake (*Trimeresurus mucrosquamatus*) venom. In peptidase family M12 (astacin family)
References: [2441, 1274]

[EC 3.4.24.54 created 1992]

EC 3.4.24.55
Accepted name: pitrilysin
Reaction: Preferential cleavage of -Tyr$^{16}$Leu- and -Phe$^{25}$Tyr-bonds of oxidized insulin B chain. Also acts on other substrates of less than 7 kDa such as insulin and glucagon
Other name(s): *Escherichia coli* protease III; protease Pi; proteinase Pi; PTR; *Escherichia coli* metalloproteinase Pi
Comments: From the periplasmic space of *Escherichia coli*. Inhibited by EDTA and 1,10-phenanthroline; not thiol-dependent. Type example of peptidase family M16
References: [686, 21, 164, 550, 46]


EC 3.4.24.56
Accepted name: insulysin
Reaction: Degradation of insulin, glucagon and other polypeptides. No action on proteins
Other name(s): insulinase; insulin-degrading enzyme; insulin protease; insulin proteinase; insulin-degrading neutral proteinase; insulin-specific protease; insulin-glucagon protease; metalloinsulinase; IDE
Comments: A 110 kDa cytosolic enzyme, known from mammals and the fruit fly, *Drosophila melanogaster*. Inhibited by bacitracin, chelating agents EDTA and 1,10-phenanthroline, and by thiol-blocking reagents such as N-ethylmaleimide, but not by phosphoramidon. In peptidase family M16 (pitrilysin family).
References: [589, 22, 590, 1353, 550]

209
EC 3.4.24.57
Accepted name: O-sialoglycoprotein endopeptidase
Reaction: Hydrolysis of O-sialoglycoproteins; cleaves -Arg-Asp- bond in glycophorin A. Does not cleave unglycosylated proteins, desialylated glycoproteins or glycoproteins that are only N-glycosylated
Other name(s): glycoprotease; glycophorin A proteinase; glycoproteinase; sialoglycoprotease; sialoglycoproteinase
Comments: An enzyme secreted by the bacterium Pasteurella haemolytica. Inhibited by EDTA (100 mM) and 1,10-phenanthroline. Type example of peptidase family M22
References: [3, 4, 2457]

EC 3.4.24.58
Accepted name: russellysin
Reaction: Specifically activates several components of the blood clotting system, including coagulation factor X, coagulation factor IX and protein C by cleavage of -Arg-bonds. Has no action on insulin B chain
Other name(s): Russell’s viper venom factor X activator, RVV-X; blood-coagulation factor X activating enzyme; metalloproteinase RVV-x; Vipera russelli protease; Russell’s viper blood coagulation factor X activator; RVV-V
Comments: This enzyme from the venom of Russell’s viper (Vipera russelli) of 79 kDa comprises a heavy (59 kDa) and a heterogeneous light (18-21 kDa) chain. Contains Ca$^{2+}$ and Zn$^{2+}$. The heavy chain contains the zinc-binding endopeptidase domain and a disintegrin. In peptidase family M12 (astacin family)
References: [769, 1471, 2504]

EC 3.4.24.59
Accepted name: mitochondrial intermediate peptidase
Reaction: Release of an N-terminal octapeptide as second stage of processing of some proteins imported into the mitochondrion
Other name(s): mitochondrial intermediate precursor-processing proteinase; MIP
Comments: A homologue of thimet oligopeptidase. Natural substrates are precursor proteins that have already been processed by mitochondrial processing peptidase. In peptidase family M3 (thimet oligopeptidase family)
References: [1096, 1097]

EC 3.4.24.60
Accepted name: dactylysin
Reaction: Hydrolysis of peptides of at least six residues, with bulky hydrophobic residues in the P1’ position. Shows a preference for hydrophobic doublets such as -Phe-Phe- and -Phe-Leu- in somatostatin-(1-14)-peptide and dynorphin A-(1-6)-peptide, respectively
Other name(s): peptide hormone inactivating endopeptidase; PHIE
Comments: An endopeptidase of 100 kDa secreted from the skin of the amphibian, Xenopus laevis (Dactylètre du Cap). Resembles neprilysin in insensitivity to 1 µM captopril, but differs from it in being insensitive to thiorphan (1 µM) and unable to digest [Met$^{5}$]enkephalin, [Leu$^{5}$]enkephalin, oxytocin, and substance P-(7-11)-peptide. A similar endopeptidase is found in human neuroblastoma cells [516]
References: [344, 516, 1164]
EC 3.4.24.61

Accepted name: nardilysin

Reaction: Hydrolysis of polypeptides, preferably at -Xaa → Arg-Lys-, and less commonly at -Arg → Arg-Xaa-, in which Xaa is not Arg or Lys

Other name(s): N-arginine dibasic convertase; NRD-convertase

Comments: Enzyme of 133 kDa from rat brain and testis. A homologue of pitrilysin containing the His-Phe-Leu-Glu-His zinc-binding sequence, and a highly acidic stretch of 71 residues. Unusually for a metalloendopeptidase, inhibited by bestatin, amastatin and N-ethylmaleimide. In peptidase family M16 (pitrilysin family)

References: [847, 829, 386, 1978]

EC 3.4.24.62

Accepted name: magnolysin

Reaction: Hydrolysis of polypeptides with Arg or Lys in P1 and P2, e.g. to hydrolyse pro-oxytocin at -Lys → Arg-Ala-Val-. The specificity further depends on the organization of a β-turn-α-helix of nine or more residues containing the paired basic amino acids near the centre [3]

Other name(s): bovine neurosecretory granule protease cleaving pro-oxytocin/neurophysin; pro-oxytocin/neurophysin convertase; prooxyphysin proteinase; pro-oxytocin convertase

Comments: An endopeptidase of 58 kDa known from bovine pituitary neurosecretory granules and bovine and human corpus luteum [1989, 886]. Inhibited by EDTA [411]

References: [411, 452, 255, 1989, 886]

EC 3.4.24.63

Accepted name: meprin B


Other name(s): meprin-b

Comments: A brush border membrane-bound metalloendopeptidase known from the intestine of all mouse strains that have been tested, and the kidney of certain inbred strains. A tetramer of meprin β subunits (in contrast to meprin A, which contains both α and β subunits). Occurs in the kidney as a proenzyme that can be activated by trypsin. Meprin B is inhibited by both EDTA and 1,10-phenanthroline, but not by phosphoramidon, captopril or thiorphan. In peptidase family M12 (astacin family)

References: [1318, 850, 1146, 2822]

EC 3.4.24.64

Accepted name: mitochondrial processing peptidase

Reaction: Release of N-terminal targetting peptides from precursor proteins imported into the mitochondrion, typically with Arg in position P2

Other name(s): processing enhancing peptidase (for one of two subunits); mitochondrial protein precursor-processing proteinase; matrix peptidase; matrix processing peptidase; matrix processing proteinase; mitochondrial protein precursor-processing proteinase; MPP

Comments: Known from the mitochondrial matrix of fungi and mammals. Formed from two subunits, both homologous with pitrilysin [2068], and the products of the MAS1 and MAS2 genes in yeast. In peptidase family M16 (pitrilysin family)

References: [1141, 2815, 2068, 1182, 297]
EC 3.4.24.65
Accepted name: macrophage elastase
Reaction: Hydrolysis of soluble and insoluble elastin [1]. Specific cleavages are also produced at -Ala
Leu-
and -Tyr-Leu- in the B chain of insulin [2]
Other name(s): metalloelastase; human macrophage metalloelastase (HME)
Comments: This enzyme is synthesized as a proenzyme of 53 kDa that is converted to an active form of 22 kDa.
cDNA sequences have been obtained for the mouse [2292] and human [2293] enzymes. In peptidase family M10 (interstitial collagenase family)
References: [119, 1242, 2292, 2293]

EC 3.4.24.66
Accepted name: choriolyisin L
Reaction: Hydrolysis of the inner layer of fish egg envelope. Also hydrolysis of casein and small molecule substrates such as succinyl-Leu-Leu-Val-Tyr-7-(4-methyl)coumarylamide
Other name(s): teleost hatching enzyme (component); low choriolytic enzyme (LCE)
Comments: Known from the teleost fish Oryzias latipes (medaka). Efficient dissolution of the egg membrane requires concerted action with choriolyisin H. A 24 kDa peptidase family M12 (astacin family)
References: [2869, 2870, 2872, 2874]

EC 3.4.24.67
Accepted name: choriolyisin H
Reaction: Hydrolysis of the inner layer of fish egg envelope. Also hydrolysis of casein and small molecule substrates such as succinyl-Leu-Leu-Val-Tyr-7-(4-methyl)coumarylamide
Other name(s): teleost hatching enzyme (component); high choriolytic enzyme (HCE)
Comments: Known from the teleost fish Oryzias latipes (medaka). Efficient dissolution of the egg membrane requires concerted action with choriolyisin L. A 25.5 kDa peptidase in family M12 (astacin family)
References: [2843, 2871, 2873, 2874, 1401]

EC 3.4.24.68
Accepted name: tentoxilysin
Reaction: Hydrolysis of -Gln-Phe- bond in synaptobrevin (also known as neuronal vesicle-associated membrane protein, VAMP)
Other name(s): tetanus neurotoxin
Comments: Zinc enzyme produced by Clostridium tetani. Proenzyme of 150 kDa is processed to disulfide-linked subunits of 100 and 50 kDa, the latter being responsible for the endopeptidase activity. Weakly inhibited by captopril, and phosphoramidon. The clostridial neurotoxins disable the neuroexocytosis apparatus, and have been described as the most toxic substances known. Tentoxilysin acts at the spinal inhibitory interneurons, blocking the release of various neurotransmitters to produce spastic paralysis. Type example of peptidase family M27 (tentoxilysin family)
References: [744, 2234, 2238, 1696, 2236]

EC 3.4.24.69

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Accepted name: bontoxilysin
Reaction: Limited hydrolysis of proteins of the neuroexocytosis apparatus, synaptobrevin (also known as neuronal vesicle-associated membrane protein, VAMP), synaptosome-associated protein of 25 kDa (SNAP25) or syntaxin. No detected action on small molecule substrates
Other name(s): botulinum neurotoxin; BoNT
Comments: This zinc enzyme, produced by *Clostridium botulinum*, occurs as forms A-G that differ in specificity of action on the proteins of the neuroexocytosis apparatus [2237, 2239, 2240, 2235, 1696]. The 150-kDa proenzymes of bontoxilysin are processed to disulfide-linked subunits of 100 and 50 kDa, the latter being responsible for the endopeptidase activities. Weakly inhibited by captopril, and phosphoramidon. Toxicity is due to action at the neuromuscular junctions that blocks release of acetylcholine, causing flaccid paralysis, in contrast to the spastic paralysis caused by tentoxilysin. In peptidase family M27 (tentoxilysin family)

References: [2237, 2239, 2240, 2235, 1696, 2236]

[EC 3.4.24.69 created 1995]

EC 3.4.24.70
Accepted name: oligopeptidase A
Reaction: Hydrolysis of oligopeptides, with broad specificity. Gly or Ala commonly occur as P1 or P1' residues, but more distant residues are also important, as is shown by the fact that Z-Gly-Pro-Gly-Gly-Pro-Ala is cleaved, but not Z-(Gly)$_5$ [4]
Other name(s): 68000-M signalpeptide hydrolase
Comments: Known from *Escherichia coli* and *Salmonella typhimurium*. A zinc metallopeptidase, in peptidase family M3 (thimet oligopeptidase family), but differs from thimet oligopeptidase in lack of thiol-activation

References: [1835, 428, 427, 426]

[EC 3.4.24.70 created 1996]

EC 3.4.24.71
Accepted name: endothelin-converting enzyme 1
Reaction: Hydrolysis of the -Trp$^{21}$+$\text{Val}$- bond in big endothelin to form endothelin 1
Other name(s): endothelin-converting enzyme; ECE-1
Comments: A phosphoramidon-sensitive metalloendopeptidase in peptidase family M13 (neprilysin family). An integral membrane protein predominantly of endothelial cells, which generates the potent vasoconstrictor endothelin 1 from its inactive precursor

References: [2485, 2302, 2836]

[EC 3.4.24.71 created 1996]

EC 3.4.24.72
Accepted name: fibrolase
Reaction: Hydrolysis of -Ala$^{14}$+$\text{Leu}$- in insulin B chain and -Lys$^{413}$+$\text{Leu}$- in Aα-chain of fibrinogen
Other name(s): fibrinolytic proteinase; *Agkistrodon contortrix contortrix* metalloproteinase; *Agkistrodon contortrix contortrix* venom metalloproteinase
Comments: A 23-kDa, non-hemorrhagic enzyme from the venom of the southern copperhead snake (*Agkistrodon contortrix contortrix*). In peptidase family M12 (astacin family)

References: [13, 884, 2057, 1491, 2099]

[EC 3.4.24.72 created 1996]

EC 3.4.24.73
Accepted name: jararhagin
Reaction: Hydrolysis of \(-\text{His}^{10}\text{-Leu}-, -\text{Ala}^{14}\text{-Leu}-, -\text{Tyr}^{16}\text{-Leu}-\text{and} -\text{Phe}^{24}\text{-Phe}-\) bonds in insulin B chain

Other name(s): HF2-proteinase; JF1

Comments: Hemorrhagic endopeptidase from the venom of the jararaca snake (\textit{Bothrops jararaca}). The 52-kDa enzyme contains a disintegrin domain [1929]. In peptidase family M12 (astacin family)

References: [1553, 76, 1929]

[EC 3.4.24.73 created 1996]

EC 3.4.24.74

Accepted name: fragilysin

Reaction: Broad proteolytic specificity, bonds hydrolysed including \(-\text{Gly}\text{-Leu}-, -\text{Met}\text{-Leu}-, -\text{Phe}\text{-Leu}-, -\text{Cys}\text{-Leu}-, \text{Leu}\text{-Gly}\)

Other name(s): \textit{Bacteroides fragilis} (entero)toxin

Comments: Thought to be a cause of diarrhoea in animals and humans. Hydrolyses extracellular matrix proteins, and disrupts tight junctions of intestinal epithelial cells. Also degrades intracellular, cytoskeletal proteins actin, myosin and others. In peptidase family M10 (interstitial collagenase family)

References: [1693, 1844, 563, 1314, 1283]

[EC 3.4.24.74 created 1997]

EC 3.4.24.75

Accepted name: lysostaphin

Reaction: Hydrolysis of the \(-\text{Gly}\text{-Gly}\)- bond in the pentaglycine inter-peptide link joining staphylococcal cell wall peptidoglycans

Other name(s): glycylyglycine endopeptidase

Comments: A zinc-dependent, 25-kDa endopeptidase from \textit{Staphylococcus simulans}. Lyses cells of \textit{S. aureus}, in particular, by its action on the cross-bridges of the cell wall. Type example of peptidase family M23.

References: [2079, 94, 2561]

[EC 3.4.24.75 created 1997]

EC 3.4.24.76

Accepted name: flavastacin

Reaction: Hydrolyses polypeptides on the amino-side of Asp in \(-\text{Xaa}\text{-Asp}-\). Acts very slowly on \(-\text{Xaa}\text{-Glu}\)

Comments: A zinc metalloendopeptidase in peptidase family M12 (astacin family), secreted by the bacterium \textit{Flavobacterium meningosepticum}. The specificity is similar to that of EC 3.4.24.33, peptidyl-Asp metalloendopeptidase from \textit{Pseudomonas fragi} but the two are reported to be structurally dissimilar

References: [2530]

[EC 3.4.24.76 created 2000]

EC 3.4.24.77

Accepted name: snapalysin

Reaction: Hydrolyses proteins with a preference for Tyr or Phe in the P1’ position. Has no action on amino-acid \(p\)-nitroanilides

Other name(s): small neutral protease; SnpA gene product (\textit{Streptomyces lividans})

Comments: Type example of peptidase family M7.

References: [1360, 307, 1359]

[EC 3.4.24.77 created 2001]

EC 3.4.24.78
Accepted name: gpr endopeptidase
Reaction: Endopeptidase action with P4 Glu or Asp, P1 preferably Glu > Asp, P1′ hydrophobic and P2′ Ala
Other name(s): germination proteinase
Comments: Initiates the degradation of small, acid-soluble proteins during spore germination in Bacillus megaterium. Type example of peptidase family M63.
References: [2003]

[EC 3.4.24.78 created 2003]

EC 3.4.24.79
Accepted name: pappalysin-1
Reaction: Cleavage of the Met\(^{135}\)→Lys bond in insulin-like growth factor binding protein (IGFBP)-4, and the Ser\(^{143}\)→Lys bond in IGFBP-5
Other name(s): insulin-like growth factor binding protein-4 protease; pregnancy-associated plasma protein-A
Comments: A 400-kDa disulfide-linked dimer. Circulates in human pregnancy mainly as a complex with the pro-form of eosinophil major basic protein, which acts as an inhibitor of the peptidase. The rate of hydrolysis of IGFBP-4 is increased about 20-fold by the presence of insulin-like growth factor (IGF), whereas that of IGFBP-5 is decreased about two-fold. In peptidase family M43.
References: [1388, 371]

[EC 3.4.24.79 created 2003]

EC 3.4.24.80
Accepted name: membrane-type matrix metalloproteinase-1
Reaction: Endopeptidase activity. Activates progelatinase A by cleavage of the propeptide at Asn\(^{37}\)→Leu. Other bonds hydrolysed include Gly\(^{35}\)→Ile in the propeptide of collagenase 3, and Asn\(^{341}\)→Phe, Asp\(^{441}\)→Leu and Gln\(^{354}\)→Thr in the aggrecan interglobular domain
Other name(s): matrix metalloproteinase 14
Comments: In peptidase family M10, but, unlike most members of the family, is membrane-anchored. Believed to play an important role in the activation of progelatinase A at cell surfaces.
References: [1106]

[EC 3.4.24.80 created 2003]

EC 3.4.24.81
Accepted name: ADAM10 endopeptidase
Reaction: Endopeptidase of broad specificity
Other name(s): Kuzbanian protein; myelin-associated disintegrin metalloproteinase
Comments: In peptidase family M12. Partially responsible for the "α-secretase" activity in brain that degrades the potentially harmful β-amyloid peptide. Work with ADAM10-deficient mice supports a role in Notch signalling.
References: [895]

[EC 3.4.24.81 created 2003]

EC 3.4.24.82
Accepted name: ADAMTS-4 endopeptidase
Reaction: Glutamyl endopeptidase; bonds cleaved include -Thr-Gly-Glu\(^{373}\)→Ala-Arg-Gly-Ser- in the interglobular domain of mammalian aggrecan
Other name(s): aggrecanase-1
Comments: In peptidase family M12. Thought to be biologically significant for the degradation of the aggrecan component of cartilage matrix.
References: [2781]

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EC 3.4.24.83

**Accepted name:** anthrax lethal factor endopeptidase

**Reaction:** Preferred amino acids around the cleavage site can be denoted BBBBxHxH, in which B denotes Arg or Lys, H denotes a hydrophobic amino acid, and x is any amino acid. The only known protein substrates are mitogen-activated protein (MAP) kinase kinases

**Other name(s):** lethal toxin

**Comments:** From the bacterium *Bacillus anthracis* that causes anthrax. One of three proteins that are collectively termed anthrax toxin. Cleaves several MAP kinase kinases near their N-termini, preventing them from phosphorylating the downstream mitogen-activated protein kinases. In peptidase family M34.

**References:** [1936]

EC 3.4.24.84

**Accepted name:** Ste24 endopeptidase

**Reaction:** The peptide bond hydrolysed can be designated -CaaX in which C is an S-isoprenylated cysteine residue, a is usually aliphatic and X is the C-terminal residue of the substrate protein, and may be any of several amino acids

**Comments:** Type example of peptidase family M48. One of two enzymes that can catalyse this processing step for mating a-factor in yeast. Subsequently, the S-isoprenylated cysteine residue that forms the new C-terminus is methyl-esterified and forms a hydrophobic membrane-anchor.

**References:** [2507]

EC 3.4.24.85

**Accepted name:** S2P endopeptidase

**Reaction:** Cleaves several transcription factors that are type-2 transmembrane proteins within membrane-spanning domains. Known substrates include sterol regulatory element-binding protein (SREBP) -1, SREBP-2 and forms of the transcriptional activator ATF6. SREBP-2 is cleaved at the site DRSRILL[483]CVLTFLCLSFNP[273]LQWGGA, in which the membrane-spanning segment is underlined. The residues NP (bold), 11 residues distal to the site of cleavage in the membrane-spanning domain, are important for cleavage by S2P endopeptidase. Replacement of either of these residues does not prevent cleavage, but there is no cleavage if both of these residues are replaced.

**Comments:** Type example of peptidase family M50. The transcription factors SREBP-1 and -2 are synthesized as precursor proteins that are attached to the membranes of the endoplasmic reticulum and two cleavages are needed to release the active factor so that it can move to the nucleus. This enzyme cleaves the second of these, and is thus the “site 2 protease”, S2P.

**References:** [287]

EC 3.4.24.86

**Accepted name:** ADAM 17 endopeptidase

**Reaction:** Narrow endopeptidase specificity. Cleaves Pro-Leu-Ala-Gln-Ala-Val-Arg-Ser-Ser-Ser in the membrane-bound, 26-kDa form of tumor necrosis factor α (TNFα). Similarly cleaves other membrane-anchored, cell-surface proteins to "shed" the extracellular domains

**Other name(s):** tumor necrosis factor α-converting enzyme; TACE

**Comments:** In peptidase family M12. In vivo, the cleavage of tumor necrosis factor α precursor releases the soluble, 17-kDa TNFα, which induces inflammation.

**References:** [206]

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**EC 3.4.24.87**

**Accepted name:** ADAMTS13 endopeptidase

**Reaction:** The enzyme cleaves the von Willebrand factor at bond Tyr$^{842}$Met$^{843}$ within the A2 domain

**Other name(s):** ADAMTS VWF cleaving metalloprotease; ADAMTS-13; ADAMTS13; vWF-cleaving protease; VWF-CP; vWF-degrading protease; Upshaw factor; von Willebrand factor cleaving protease; ADAMTS13 peptidase

**Comments:** In peptidase family M12.

**References:** [750, 564]

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**EC 3.4.25 Threonine endopeptidases**

**EC 3.4.25.1**

**Accepted name:** proteasome endopeptidase complex

**Reaction:** Cleavage of peptide bonds with very broad specificity

**Other name(s):** ingensin; macropain; multicatalytic endopeptidase complex; prosome; multicatalytic proteinase (complex); MCP; proteasome; large multicatalytic protease; multicatalytic proteinase; proteasome organelle; alkaline protease; 26S protease; tricorn proteinase; tricorn protease

**Comments:** A 20-S protein composed of 28 subunits arranged in four rings of seven. The outer rings are composed of α subunits, but the β subunits forming the inner rings are responsible for peptidase activity. In eukaryotic organisms there are up to seven different types of β subunits, three of which may carry the N-terminal threonine residues that are the nucleophiles in catalysis, and show different specificities. The molecule is barrel-shaped, and the active sites are on the inner surfaces. Terminal apertures restrict access of substrates to the active sites. There is evidence that catalytic subunits are replaced by others under some conditions so as to alter the specificity of proteolysis, perhaps optimizing it for the formation of antigenic peptides. A complex of the 20-S proteasome endopeptidase complex with a 19-S regulatory unit is the 26-S proteasome that degrades ubiquitin-protein conjugates. Type example of peptidase family T1.

**References:** [2269, 448, 879, 537]

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**EC 3.4.25.2**

**Accepted name:** HslU—HslV peptidase

**Reaction:** ATP-dependent cleavage of the cell division inhibitor SulA. The central and the C-terminal regions are preferentially cleaved. Major cleavage sites: Ala$^{80}$Ser$^{81}$, Ala$^{150}$Ser$^{151}$, Leu$^{54}$Gln$^{55}$, Ile$^{163}$His$^{164}$, Leu$^{67}$Thr$^{68}$, Leu$^{49}$Leu$^{50}$, Leu$^{65}$Trp$^{66}$.

**Other name(s):** ClpQ; ClpYQ; ClpYQ protease; HslUV; HslV-HslU; HslV peptidase; ATP-dependent HslV-HslU proteinase; caseinolytic protease X; caseinolytic proteinase X; ClpXP ATP-dependent protease; ClpXP protease; ClpXP serine proteinase; *Escherichia coli* ClpXP serine proteinase; HslUV protease; HslUV proteinase; HslUV protease; HslUV proteinase; protease ClpYQ; protease CodWX; protease HslUV; proteinase ClpYQ; proteinase HslUV

**Comments:** In peptidase family T1.

**References:** [2733, 1813, 2049, 2886]

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[EC 3.4.24.86 created 2003]

[EC 3.4.25.1 created 1978 as EC 3.4.24.5, part transferred 1989 to EC 3.4.22.21, transferred 1992 to EC 3.4.99.46, transferred 2000 to EC 3.4.25.1]

[EC 3.4.25.2 created 2009]
EC 3.4.99 Endopeptidases of unknown catalytic mechanism (sub-subclass is currently empty)

[3.4.99.1 Transferred entry. acrocyldricum proteinase. Now EC 3.4.23.28, acrocyldropepsin]
[EC 3.4.99.1 created 1972, deleted 1978 [transferred to EC 3.4.23.6, deleted 1992]]

[3.4.99.2 Deleted entry. agavain]
[EC 3.4.99.2 created 1972, deleted 1992]

[3.4.99.3 Deleted entry. angiotensinase]
[EC 3.4.99.3 created 1972, deleted 1992]

[3.4.99.4 Transferred entry. aspartylendopeptidase. Now EC 3.4.23.12, nepenthesin]
[EC 3.4.99.4 created 1972, deleted 1978]

[3.4.99.5 Transferred entry. Clostridium histolyticum collagenase 2. Now EC 3.4.24.3, microbial collagenase]
[EC 3.4.99.5 created 1972, deleted 1978]

[3.4.99.6 Transferred entry. crayfish low-molecular-weight proteinase. Now EC 3.4.24.21, astacin]
[EC 3.4.99.6 created 1972, deleted 1992]

[3.4.99.7 Deleted entry. euphorbain]
[EC 3.4.99.7 created 1972, deleted 1989]

[3.4.99.8 Deleted entry. Gliocladium proteinase]
[EC 3.4.99.8 created 1972, deleted 1992]

[3.4.99.9 Deleted entry. hurain]
[EC 3.4.99.9 created 1972, deleted 1992]

[3.4.99.10 Transferred entry. insulinsinase. Now EC 3.4.24.56, insulysin]
[EC 3.4.99.10 created 1972, transferred 1976 to EC 3.4.22.11, transferred 1978 to EC 3.4.99.45, transferred 1993 to EC 3.4.24.56]

[3.4.99.11 Deleted entry. Streptomyces alkalophilic keratinase]
[EC 3.4.99.11 created 1965 as EC 3.4.4.25, transferred 1972 to EC 3.4.99.11, deleted 1992]

[3.4.99.12 Deleted entry. Trichophyton mentagrophytes keratinase]
[EC 3.4.99.12 created 1972, deleted 1978 [transferred to EC 3.4.24.10, deleted 1992]]

[EC 3.4.99.13 created 1972, deleted 1978 [transferred to EC 3.4.24.4, deleted 1992]]

[3.4.99.14 Deleted entry. mexicanain]
[EC 3.4.99.14 created 1972, deleted 1992]

[3.4.99.15 Deleted entry. Paecilomyces proteinase]
[EC 3.4.99.15 created 1972, deleted 1978 [transferred to EC 3.4.23.6, deleted 1992]]

[3.4.99.16 Deleted entry. Penicillium notatum extracellular proteinase]
[EC 3.4.99.16 created 1972, deleted 1992]

[3.4.99.17 Deleted entry. peptidoglycan endopeptidase]
3.4.99.18 Deleted entry. pinguinain

3.4.99.19 Transferred entry. renin. Now EC 3.4.23.15, renin

3.4.99.20 Deleted entry. Scopulariopsis proteinase

3.4.99.21 Deleted entry. solanain

3.4.99.22 Transferred entry. staphylokinase. Now EC 3.4.24.29, aureolysin

3.4.99.23 Deleted entry. tabernamontanain

3.4.99.24 Deleted entry. Tenebrio α-proteinase

3.4.99.25 Transferred entry. trametes acid proteinase. Now EC 3.4.23.21, rhizopuspepsin

3.4.99.26 Transferred entry. urokinase. Now EC 3.4.21.68, t-plasminogen activator

3.4.99.27 Deleted entry. Echis carinatus prothrombin-activating proteinase

3.4.99.28 Transferred entry. Oxyuranus scutellatus prothrombin-activating proteinase. Now EC 3.4.21.60, scutelarin

3.4.99.29 Deleted entry. Myxobacter AL-I proteinase I

3.4.99.30 Transferred entry. Myxobacter AL-I proteinase II. Now EC 3.4.24.20, peptidyl-Lys metalloendopeptidase

3.4.99.31 Transferred entry. tissue endopeptidase degrading collagenase synthetic substrate. Now EC 3.4.24.15, thimet oligopeptidase


3.4.99.33 Deleted entry. cathepsin R

3.4.99.34 Deleted entry. mytilidase
EC 3.4.99.34 created 1981, deleted 1992


[EC 3.4.99.35 created 1984, deleted 1995]


[EC 3.4.99.36 created 1984, deleted 1995]

[3.4.99.37] Deleted entry. RecA peptidase

[EC 3.4.99.37 created 1989, deleted 1992]

[3.4.99.38] Transferred entry. pro-opiomelanotropin-converting proteinase. Now EC 3.4.23.17, pro-opiomelanocortin converting enzyme

[EC 3.4.99.38 created 1989, deleted 1992]

[3.4.99.39] Deleted entry. pseudomurein endopeptidase


[3.4.99.40] Deleted entry. Pro-gonadoliberin proteinase

[EC 3.4.99.40 created 1989, deleted 1992]

[3.4.99.41] Transferred entry. mitochondrial processing peptidase. Now EC 3.4.24.64, mitochondrial processing peptidase

[EC 3.4.99.41 created 1989/90, deleted 1995]

[3.4.99.42] Deleted entry. leucyllysine endopeptidase

[EC 3.4.99.42 created 1990, deleted 1992]

[3.4.99.43] Transferred entry. thermopsin. Now EC 3.4.23.42, thermopsin

[EC 3.4.99.43 created 1992, deleted 2000]


[EC 3.4.99.44 created 1992, deleted 1993]


[EC 3.4.99.45 created 1992, deleted 1993]


[EC 3.4.99.46 created 1992, deleted 2000]

EC 3.5 Acting on carbon-nitrogen bonds, other than peptide bonds

This subclass contains those enzymes that hydrolyse amides, amidines and other C-N bonds. Sub-subclasses are based on the substrate: linear amides (EC 3.5.1), cyclic amides (EC 3.5.2), linear amidines (EC 3.5.3), cyclic amidines (EC 3.5.4), nitriles (EC 3.5.5) and other compounds (EC 3.5.99).

EC 3.5.1 In linear amides

EC 3.5.1.1

Accepted name: asparaginase

Reaction: L-asparagine + H₂O = L-aspartate + NH₃

Other name(s): asparaginase II; L-asparaginase; colaspase; elspar; leunase; crasnitin; α-asparaginase

Systematic name: L-asparagine amidohydrolase

References: [912, 1018, 2445]
EC 3.5.1.1
Accepted name: glutaminase
Reaction: L-glutamine + H₂O = L-glutamate + NH₃
Other name(s): glutaminase I; L-glutaminase; glutamine aminohydrolase
Systematic name: L-glutamine amidohydrolase
References: [1345, 2122]

EC 3.5.1.2
Accepted name: glutaminase
Reaction: L-glutamine + H₂O = L-glutamate + NH₃
Other name(s): glutaminase I; L-glutaminase; glutamine aminohydrolase
Systematic name: L-glutamine amidohydrolase
References: [1345, 2122]

EC 3.5.1.3
Accepted name: ω-amidase
Reaction: a monoamide of a dicarboxylic acid + H₂O = a dicarboxylate + NH₃
Other name(s): α-keto acid-ω-amidase
Systematic name: ω-amidodicarboxylate amidohydrolase
References: [1632, 1633]

EC 3.5.1.4
Accepted name: amidase
Reaction: a monocarboxylic acid amide + H₂O = a monocarboxylate + NH₃
Other name(s): acylamidase; acylase; amidohydrolase; deaminase; fatty acylamidase; N-acetylaminohydrolase
Systematic name: acylamide amidohydrolase
References: [258, 259]

EC 3.5.1.5
Accepted name: urease
Reaction: urea + H₂O = CO₂ + 2 NH₃
Systematic name: urea amidohydrolase
Comments: A nickel protein.
References: [551, 2448, 2682]

EC 3.5.1.6
Accepted name: β-ureidopropionase
Reaction: N-carbamoyl-β-alanine + H₂O = β-alanine + CO₂ + NH₃
Systematic name: N-carbamoyl-β-alanine amidohydrolase
Comments: The animal enzyme also acts on β-ureidoisobutyrate.
References: [331, 338, 2594]

EC 3.5.1.7
Accepted name: ureidosuccinase
Reaction: N-carbamoyl-L-aspartate + H₂O = L-aspartate + CO₂ + NH₃
Systematic name: N-carbamoyl-L-aspartate amidohydrolase
EC 3.5.1.8

Accepted name: formylaspartate deformylase
Reaction: \( N\text{-formyl-L-aspartate} + H_2O = \text{formate} + \text{L-aspartate} \)
Other name(s): formylaspartic formylase (formylase I, formylase II)
Systematic name: \( N\text{-formyl-L-aspartate amidohydrolase} \)
References: [1878]

[EC 3.5.1.8 created 1961]

EC 3.5.1.9

Accepted name: arylformamidase
Reaction: \( N\text{-formyl-L-kynurenine} + H_2O = \text{formate} + \text{L-kynurenine} \)
Other name(s): kynurenine formamidase; formylase; formylkynureninase; formylkynurenine formamidase; formamidase I; formamidase II
Systematic name: aryl-formylamine amidohydrolase
Comments: Also acts on other aromatic formylamines.
References: [960, 1124, 1629]

[EC 3.5.1.9 created 1961]

EC 3.5.1.10

Accepted name: formyltetrahydrofolate deformylase
Reaction: \( 10\text{-formyltetrahydrofolate} + H_2O = \text{formate} + \text{tetrahydrofolate} \)
Systematic name: 10-formyltetrahydrofolate amidohydrolase
References: [1059]

[EC 3.5.1.10 created 1961]

EC 3.5.1.11

Accepted name: penicillin amidase
Reaction: \( \text{penicillin} + H_2O = \text{a carboxylate} + 6\text{-aminopenicillanate} \)
Other name(s): penicillin acylase; benzylpenicillin acylase; novozym 217; semacylase; \( \alpha\)-acylamino-\( \beta\)-lactam acylhydrolase; ampicillin acylase
Systematic name: penicillin amidohydrolase
References: [2185]

[EC 3.5.1.11 created 1961]

EC 3.5.1.12

Accepted name: biotinidase
Reaction: \( \text{biotin amide} + H_2O = \text{biotin} + \text{NH}_3 \)
Other name(s): amidohydrolase biotinidase
Systematic name: biotin-amide amidohydrolase
Comments: Also acts on biotin esters.
References: [1284, 2550]

[EC 3.5.1.12 created 1961]
EC 3.5.1.13
Accepted name: aryl-acylamidase
Reaction: an anilide + H₂O = a carboxylate + aniline
Other name(s): AAA-1; AAA-2; brain acetylcholinesterase (is associated with AAA-2); pseudocholinesterase (associated with arylacylamidase)
Systematic name: aryl-acylamide amidohydrolase
Comments: Also acts on 4-substituted anilides.
References: [1811]

[EC 3.5.1.13 created 1965]

EC 3.5.1.14
Accepted name: aminoacylase
Reaction: an N-acyl-L-amino acid + H₂O = a carboxylate + an L-amino acid
Other name(s): dehydropeptidase II; histozyme; hippuricase; benzamidase; acylase I; hippurase; amido acid deacylase; L-aminoacylase; acylase; aminoacylase I; L-amino-acid acylase; α-N-acylaminoacid hydrolase; long acyl amidoacylase; short acyl amidoacylase
Systematic name: N-acyl-L-amino-acid amidohydrolase
Comments: Wide specificity; also hydrolyses dehydropeptides. Used in separating D- and L- amino acids
References: [198, 713, 1939]

[EC 3.5.1.14 created 1965]

EC 3.5.1.15
Accepted name: aspartoacylase
Reaction: N2-acyl-L-ornithine + H₂O = acetate + L-ornithine
Other name(s): acetylornithinase; N-acylornithinase; 2-N-acetyl-L-ornithine amidohydrolase
Systematic name: N²-acyl-L-ornithine amidohydrolase
Comments: Also hydrolyses N-acetylmethionine.
References: [2699, 2700]

[EC 3.5.1.15 created 1965]

EC 3.5.1.16
Accepted name: acetylornithine deacetylase
Reaction: N²-acyl-L-ornithine + H₂O = acetate + L-ornithine
Other name(s): acetylornithinase; N-acetylornithinase; 2-N-acetyl-L-ornithine amidohydrolase
Systematic name: N²-acyl-L-ornithine amidohydrolase
Comments: Also hydrolyses N-acetylmethionine.
References: [2699, 2700]

[EC 3.5.1.16 created 1965]

EC 3.5.1.17
Accepted name: acyl-lysine deacylase
Reaction: N⁶-acyl-L-lysine + H₂O = a carboxylate + L-lysine
Other name(s): ε-lysine acylase; 6-N-acyl-L-lysine amidohydrolase
Systematic name: N⁶-acyl-L-lysine amidohydrolase
References: [1928]

[EC 3.5.1.17 created 1965]

EC 3.5.1.18
Accepted name: succinyl-diaminopimelate desuccinylase
Reaction: $N$-succinyl-LL-2,6-diaminoheptanedioate + $H_2O =$ succinate + LL-2,6-diaminoheptanedioate
Other name(s): $N$-succinyl-$\alpha,\varepsilon$-diaminopimelic acid deacylase
Systematic name: $N$-succinyl-LL-2,6-diaminoheptanedioate amidohydrolase
References: [1266]

[EC 3.5.1.18 created 1965]

EC 3.5.1.19
Accepted name: nicotinamidase
Reaction: nicotinamide + $H_2O =$ nicotinate + $NH_3$
Other name(s): nicotinamide deaminase; nicotinamide amidase; YNDase
Systematic name: nicotinamide amidohydrolase
References: [1965, 2210]

[EC 3.5.1.19 created 1972]

EC 3.5.1.20
Accepted name: citrullinase
Reaction: L-citrulline + $H_2O =$ L-ornithine + $CO_2 + NH_3$
Other name(s): citrulline ureidase; citrulline hydrolase; L-citrulline 5-N-carbamoyldihydrolase
Systematic name: L-citrulline $N^5$-carbamoyldihydrolase
References: [1006]

[EC 3.5.1.20 created 1972]

EC 3.5.1.21
Accepted name: $N$-acetyl-$\beta$-alanine deacetylase
Reaction: $N$-acetyl-$\beta$-alanine + $H_2O =$ acetate + $\beta$-alanine
Systematic name: $N$-acetyl-$\beta$-alanine amidohydrolase
References: [751]

[EC 3.5.1.21 created 1972]

EC 3.5.1.22
Accepted name: pantothenase
Reaction: $(R)$-pantothenate + $H_2O = (R)$-pantoate + $\beta$-alanine
Other name(s): pantothenate hydrolase; pantothenate amidohydrolase
Systematic name: $(R)$-pantothenate amidohydrolase
References: [1840]

[EC 3.5.1.22 created 1972]

EC 3.5.1.23
Accepted name: ceramidase
Reaction: $N$-acylsphingosine + $H_2O =$ a carboxylate + sphingosine
Other name(s): acylsphingosine deacylase; glycosphingolipid ceramide deacylase
Systematic name: $N$-acylsphingosine amidohydrolase
References: [1809, 2876]

[EC 3.5.1.23 created 1972, modified 1990]
EC 3.5.1.24

Accepted name: choloylglycine hydrolase

Reaction: \(3\alpha,7\alpha,12\alpha\text{-trihydroxy-5}\beta\text{-cholan-24-oylglycine} + H_2O = 3\alpha,7\alpha,12\alpha\text{-trihydroxy-5}\beta\text{-cholanate} + \text{glycine}\)

Other name(s): glycocholase; bile salt hydrolase; choloyltaurine hydrolase

Systematic name: \(3\alpha,7\alpha,12\alpha\text{-trihydroxy-5}\beta\text{-cholan-24-oylglycine amidohydrolase}\)

Comments: Also acts on the \(3\alpha,12\alpha\text{-dihydroxy-derivative, and on choloyl-taurine.}\)

References: [1759, 2419]

[EC 3.5.1.24 created 1972]

EC 3.5.1.25

Accepted name: \(N\text{-acetylglucosamine-6-phosphate deacetylase}\)

Reaction: \(N\text{-acetyl-D-glucosamine 6-phosphate} + H_2O = \text{D-glucosamine 6-phosphate} + \text{acetate}\)

Other name(s): acetylglucosamine phosphate deacetylase; acetylaminodeoxyglucosephosphate acetylhydrolase; 2-acetamido-2-deoxy-D-glucose-6-phosphate amidohydrolase

Systematic name: \(N\text{-acetyl-D-glucosamine-6-phosphate amidohydrolase}\)

References: [2790, 2850]

[EC 3.5.1.25 created 1972 (EC 3.5.1.80 created 1999, incorporated 2002)]

EC 3.5.1.26

Accepted name: \(N^4\text{-} (\beta\text{-N-acetylglucosaminyl})\text{-L-asparaginase}\)

Reaction: \(N^4\text{-}(\beta\text{-N-acetyl-D-glucosaminyl})\text{-L-asparagine} + H_2O = N\text{-acetyl-\beta-D-glucosaminylamine} + \text{L-aspartate}\)

Other name(s): aspartylglucosylamine deaspartylase; aspartylglucosylaminase; aspartylglucosaminidase; aspartylglycosylamine amidohydrolase; \(N\text{-aspartyl-\beta-D-glucosaminidase; glucosylamidase; \beta-aspartylglucosylamine amidohydrolase; 4-N-(\beta\text{-N-acetyl-D-glucosaminyl})-L-asparagine amidohydrolase}\)

Systematic name: \(N^4\text{-}(\beta\text{-N-acetyl-D-glucosaminyl})\text{-L-asparagine amidohydrolase}\)

Comments: Acts only on asparagine-oligosaccharides containing one amino acid, i.e., the asparagine has free \(\alpha\)-amino and \(\alpha\)-carboxyl groups [cf. EC 3.5.1.52, peptide-\(N^4\text{-}(N\text{-acetyl-\beta-D-glucosaminyl)asparagine amidase}]]

References: [1298, 1530, 2528]

[EC 3.5.1.26 created 1972 (EC 3.5.1.37 created 1972, incorporated 1976)]

EC 3.5.1.27

Accepted name: \(N\text{-formylmethionylaminoacyl-tRNA deformylase}\)

Reaction: \(N\text{-formyl-L-methionylaminoacyl-tRNA} + H_2O = \text{formate} + \text{L-methionylaminoacyl-tRNA}\)

Systematic name: \(N\text{-formyl-L-methionylaminoacyl-tRNA amidohydrolase}\)

References: [1488]

[EC 3.5.1.27 created 1972]

EC 3.5.1.28

Accepted name: \(N\text{-acetylmuramoyl-L-alanine amidase}\)

Reaction: Hydrolyses the link between \(N\text{-acetylmuramoyl residues and L-amino acid residues in certain cell-wall glycopeptides}\)

Other name(s): acetylmuramyl-L-alanine amidase; \(N\text{-acetylmuramyl-L-alanine amidase; \(N\text{-acylmuramyloyl-L-alanine amidase; acetylmuramoyloyl-L-alanine amidase; N-acytelymuramone acid L-alanine amidase; acetylmuramyl-alanine amidase; N-acetylmuramylalanine amidase; murein hydrolase; N-acetylmuramoyloyl-L-alanine amidase type I; N-acetylmuramoyloyl-L-alanine amidase type II}\)
Systematic name: peptidoglycan amidohydrolase
References: [804, 994, 993, 2744]

[EC 3.5.1.28 created 1972 (EC 3.4.19.10 created 1992, incorporated 1997)]

EC 3.5.1.29
Accepted name: 2-(acetamidomethylene)succinate hydrolase
Reaction: 2-(acetamidomethylene)succinate + 2 H₂O = acetate + succinate semialdehyde + NH₃ + CO₂
Other name(s): α-(N-acetylaminomethylene)succinic acid hydrolase
Systematic name: 2-(acetamidomethylene)succinate amidohydrolase (deaminating, decarboxylating)
Comments: Involved in the degradation of pyridoxin in Pseudomonas.
References: [1064, 1843]

[EC 3.5.1.29 created 1972]

EC 3.5.1.30
Accepted name: 5-aminopentanamidase
Reaction: 5-aminopentanamide + H₂O = 5-aminopentanoate + NH₃
Other name(s): 5-aminovaleramidase; 5-aminonorvaleramidase
Systematic name: 5-aminopentanamide amidohydrolase
Comments: The enzyme from Pseudomonas putida also acts on 4-aminobutanamide and, more slowly, on 6-aminohexanamide.
References: [2092, 2499]

[EC 3.5.1.30 created 1972, modified 1976]

EC 3.5.1.31
Accepted name: formylmethionine deformylase
Reaction: N-formyl-L-methionine + H₂O = formate + L-methionine
Systematic name: N-formyl-L-methionine amidohydrolase
References: [68]

[EC 3.5.1.31 created 1972]

EC 3.5.1.32
Accepted name: hippurate hydrolase
Reaction: hippurate + H₂O = benzoate + glycine
Systematic name: N-benzyolamino-acid amidohydrolase
Comments: Acts on various N-benzyolamino acids.
References: [2138, 2139, 2140]

[EC 3.5.1.32 created 1972]

EC 3.5.1.33
Accepted name: N-acetylglucosamine deacetylase
Reaction: N-acetyl-D-glucosamine + H₂O = D-glucosamine + acetate
Other name(s): acetylamino deoxyglucose acetylhydrolase; N-acetyl-D-glucosaminyl N-deacetylase
Systematic name: N-acetyl-D-glucosamine amidohydrolase
References: [2145]

[EC 3.5.1.33 created 1972]
EC 3.5.1.35
Accepted name: D-glutaminase
Reaction: D-glutamine + H₂O = D-glutamate + NH₃
Systematic name: D-glutamine amidohydrolase
References: [562]

EC 3.5.1.36
Accepted name: N-methyl-2-oxoglutaramate hydrolase
Reaction: N-methyl-2-oxoglutarate + H₂O = 2-oxoglutarate + methylamine
Other name(s): 5-hydroxy-N-methylpyroglutamate synthase
Systematic name: N-methyl-2-oxoglutarate methylamidohydrolase
Comments: In the reverse reaction, the product cyclizes non-enzymically to 2-hydroxy-N-methyl-5-oxopropionate.
References: [999, 1000]

EC 3.5.1.37
Deleted entry. 4-L-aspartylglycosylamine amidohydrolase. Identical with EC 3.5.1.26 N⁴-[β-N-acetylglucosaminil]-L-asparaginase

EC 3.5.1.38
Accepted name: glutamin-(asparagin-)ase
Reaction: L-glutamine + H₂O = L-glutamate + NH₃
Systematic name: L-glutamine(L-asparagine) amidohydrolase
Comments: L-Asparagine is hydrolysed at 0.8 of the rate of L-glutamine; the D-isomers are also hydrolysed, but more slowly.
References: [2123]

EC 3.5.1.39
Accepted name: alkylamidase
Reaction: N-methylhexanamide + H₂O = hexanoate + methylamine
Systematic name: N-methylhexanamide amidohydrolase
Comments: The enzyme hydrolyses N-monosubstituted and N,N-disubstituted amides, and there is some activity towards primary amides. It has little or no activity towards short-chain substrates.
References: [377]

EC 3.5.1.40
Accepted name: acylagmatine amidase
Reaction: benzoylagmatine + H₂O = benzoate + agmatine
Other name(s): acylagmatine amidohydrolase; acylagmatine deacylase
Systematic name: benzoylagmatine amidohydrolase
Comments: Also acts on acetylagmatine, propanoylagmatine and bleomycin B2
References: [2640]
EC 3.5.1.40 created 1976

EC 3.5.1.41
Accepted name: chitin deacetylase
Reaction: chitin + H₂O = chitosan + acetate
Systematic name: chitin amidohydrolase
Comments: Hydrolyses the N-acetamido groups of N-acetyl-D-glucosamine residues in chitin.
References: [62]

EC 3.5.1.42
Accepted name: nicotinamide-nucleotide amidase
Reaction: β-nicotinamide D-ribonucleotide + H₂O = β-nicotinate D-ribonucleotide + NH₃
Other name(s): NMN deamidase; nicotinamide mononucleotide deamidase; nicotinamide mononucleotide amidohydrolase
Systematic name: nicotinamide-D-ribonucleotide amidohydrolase
Comments: Also acts more slowly on β-nicotinamide D-ribonucleoside.
References: [1081]

EC 3.5.1.43
Accepted name: peptidyl-glutaminase
Reaction: α-N-peptidyl-L-glutamine + H₂O = α-N-peptidyl-L-glutamate + NH₃
Other name(s): peptidoglutaminase I; peptideglutaminase; peptidoglutaminase
Systematic name: peptidyl-L-glutamine amidohydrolase
Comments: Specific for the hydrolysis of the γ-amide of glutamine substituted at the α-amino group, e.g., glycyl-L-glutamine, N-acetyl-L-glutamine and L-leucylglycyl-L-glutamine.
References: [1251]

EC 3.5.1.44
Accepted name: protein-glutamine glutaminase
Reaction: protein L-glutamine + H₂O = protein L-glutamate + NH₃
Other name(s): peptidoglutaminase II; glutaminyl-peptide glutaminase; destabilase; peptidylglutaminase II
Systematic name: protein-L-glutamine amidohydrolase
Comments: Specific for the hydrolysis of the γ-amide of glutamine substituted at the carboxyl position or both the α-amino and carboxyl positions, e.g., L-glutaminylglycine and L-phenylalanyl-L-glutaminylglycine.
References: [1251]

EC 3.5.1.46
Accepted name: 6-aminohexanoate-dimer hydrolase
Reaction: N-(6-aminohexanoyl)-6-aminohexanoate + H₂O = 2 6-aminohexanoate
Other name(s): 6-aminohexanoic acid oligomer hydrolase
Systematic name: N-(6-aminohexanoyl)-6-aminohexanoate amidohydrolase

[EC 3.5.1.41 created 1976]

[EC 3.5.1.42 created 1976]

[EC 3.5.1.43 created 1976]

[EC 3.5.1.44 created 1976, modified 1983]

[3.5.1.45 Deleted entry. urease (ATP-hydrolysing). Now listed only as EC 6.3.4.6 urea carboxylase]

[EC 3.5.1.45 created 1978, deleted 1986]
Comments: Also hydrolyses oligomers of 6-aminohexanoate containing up to six residues, but more slowly; the residues are removed sequentially from the N-terminus.

References: [1268]

[EC 3.5.1.46 created 1983]

EC 3.5.1.47

Accepted name: N-acetyldiaminopimelate deacetylase
Reaction: \( \text{N-acetyl-LL-2,6-diaminoheptanedioate} + \text{H}_2\text{O} = \text{acetate} + \text{LL-2,6-diaminoheptanedioate} \)
Other name(s): N-acetyl-L-diaminopimelic acid deacetylase; N-acetyl-LL-diaminopimelate deacetylase; 6-N-acetyl-LL-2,6-diaminoheptanedioate amidohydrolase
Systematic name: \( \text{N}^6\)-acetyl-LL-2,6-diaminoheptanedioate amidohydrolase
References: [147, 2192, 2452]

[EC 3.5.1.47 created 1984 (EC 3.1.1.62 created 1989, incorporated 1992)]

EC 3.5.1.48

Accepted name: acetylspermidine deacetylase
Reaction: \( \text{N}^8\)-acetylspermidine + \text{H}_2\text{O} = \text{acetate} + \text{spermidine} \)
Other name(s): \( \text{N}^8\)-monoacetylspermidine deacetylase; \( \text{N}^8\)-acetylspermidine deacetylase; \( \text{N}^1\)-acetylspermidine amidohydrolase (incorrect); 8-N-acetylspermidine amidohydrolase
Systematic name: \( \text{N}^8\)-acetylspermidine amidohydrolase
Comments: It was initially thought that \( \text{N}^1\)-acetylspermidine was the substrate for this deacetylase reaction [1452] but this has since been disproved by Marchant et al. [1560].
References: [1452, 221, 1560]

[EC 3.5.1.48 created 1984, modified 2005]

EC 3.5.1.49

Accepted name: formamidase
Reaction: formamide + \text{H}_2\text{O} = \text{formate} + \text{NH}_3 \)
Systematic name: formamide amidohydrolase
Comments: Also acts, more slowly, on acetamide, propanamide and butanamide.
References: [413, 735]

[EC 3.5.1.49 created 1984]

EC 3.5.1.50

Accepted name: pentanamidase
Reaction: pentanamide + \text{H}_2\text{O} = \text{pentanoate} + \text{NH}_3 \)
Other name(s): valeramidase
Systematic name: pentanamide amidohydrolase
Comments: Also acts, more slowly, on other short-chain aliphatic amides. Different from EC 3.5.1.49 formamidase.
References: [735]

[EC 3.5.1.50 created 1984]

EC 3.5.1.51

Accepted name: 4-acetamidobutyryl-CoA deacetylase
Reaction: \( \text{4-acetamidobutyryl-CoA} + \text{H}_2\text{O} = \text{acetate} + \text{4-aminobutanoyl-CoA} \)
Other name(s): aminobutyryl-CoA thiolesterase; deacetylase-thiolesterase

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Systematic name: 4-acetamidobutanoyl-CoA amidohydrolase
Comments: The enzyme also hydrolyses 4-aminobutanoyl-CoA to aminobutanoate and coenzyme A.
References: [1880]

[EC 3.5.1.51 created 1984]

EC 3.5.1.52
Accepted name: peptide-$N^4$-(N-acetyl-$\beta$-glucosaminyl)asparagine amidase
Reaction: Hydrolysis of an $N^4$-(acetyl-$\beta$-glucosaminyl)asparagine residue in which the glucosamine residue may be further glycosylated, to yield a (substituted) $N$-acetyl-$\beta$-D-glucosaminylamine and a peptide containing an aspartate residue
Other name(s): glycopeptide $N$-glycosidase; glycopeptidase; $N$-oligosaccharide glycopeptidase; $N$-glycanase; Jack-bean glycopeptidase; PNGase A; PNGase F
Systematic name: N-linked-glycopeptide-(N-acetyl-$\beta$-D-glucosaminyl)-L-asparagine amidohydrolase
Comments: Does not act on (GlcNAc)Asn, because it requires the presence of more than two amino-acid residues in the substrate [cf. EC 3.5.1.26, $N^4$-(β-$N$-acetylglucosaminyl)-L-asparaginase]. The plant enzyme was previously erroneously listed as EC 3.2.2.18.
References: [1991, 2486, 2488, 2527]

[EC 3.5.1.52 created 1984, modified 1989 (EC 3.2.2.18 created 1984, incorporated 1989)]

EC 3.5.1.53
Accepted name: $N$-carbamoylputrescine amidase
Reaction: $N$-carbamoylputrescine + $H_2O = putrescine + CO_2 + NH_3$
Other name(s): carbamoylputrescine hydrolase; NCP
Systematic name: $N$-carbamoylputrescine amidohydrolase
References: [2853]

[EC 3.5.1.53 created 1986]

EC 3.5.1.54
Accepted name: allophanate hydrolase
Reaction: urea-1-carboxylate + $H_2O = 2 CO_2 + 2 NH_3$
Other name(s): allophanate lyase; AtzF; TrzF
Systematic name: urea-1-carboxylate amidohydrolase
Comments: Along with EC 3.5.2.15 (cyanuric acid amidohydrolase) and EC 3.5.1.84 (biuret amidohydrolase), this enzyme forms part of the cyanuric-acid metabolism pathway, which degrades s-triazide herbicides, such as atrazine [2-chloro-4-(ethylamino)-6-(isopropylamino)-1,3,5-triazine], in bacteria. The yeast enzyme (but not that from green algae) also catalyses the reaction of EC 6.3.4.6, urea carboxylase, thus bringing about the hydrolysis of urea to CO$_2$ and NH$_3$ in the presence of ATP and bicarbonate. The enzyme from Pseudomonas sp. strain ADP has a narrow substrate specificity, being unable to use the structurally analogous compounds urea, hydroxyurea or methylcarbamate as substrate [2288].
References: [1538, 2142, 2449, 1191, 383, 2288, 2287]

[EC 3.5.1.54 created 1986, modified 2008]

EC 3.5.1.55
Accepted name: long-chain-fatty-acyl-glutamate deacylase
Reaction: $N$-long-chain-fatty-acyl-L-glutamate + $H_2O = a$ long-chain carboxylate + L-glutamate
Other name(s): long-chain aminoacylase; long-chain-fatty-acyl-glutamate deacylase; long-chain acylglutamate amidase; $N$-acyl-$\beta$-D-glutamate deacylase
Systematic name: $N$-long-chain-fatty-acyl-L-glutamate amidohydrolase
Comments: Does not act on acyl derivates of other amino acids. Optimum chain length of acyl residue is 12 to 16.
References: [762]

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EC 3.5.1.56

**Accepted name:** N,N-dimethylformamidase  
**Reaction:** N,N-dimethylformamide + H₂O = dimethylamine + formate  
**Other name(s):** dimethylformamidase; DMFase  
**Systematic name:** N,N-dimethylformamide amidohydrolase  
**Comments:** An iron protein. Also acts on N-ethylformamide and N-methyl-formamide and, more slowly, on N,N-diethylformamide, N,N-dimethylacetamide and unsubstituted acyl amides.  
**References:** [2230]

[EC 3.5.1.56 created 1989]

EC 3.5.1.57

**Accepted name:** tryptophanamidase  
**Reaction:** L-tryptophanamide + H₂O = L-tryptophan + NH₃  
**Other name(s):** tryptophan aminopeptidase; L-tryptophan aminopeptidase  
**Systematic name:** L-tryptophanamide amidohydrolase  
**Comments:** Requires Mn²⁺. Also acts on N-ethylformamide and L-tyrosinamide, and on some tryptophan dipeptides.  
**References:** [1110]

[EC 3.5.1.57 created 1989]

EC 3.5.1.58

**Accepted name:** N-benzyloxy carbonylglycine hydrolase  
**Reaction:** N-benzyloxy carbonylglycine + H₂O = benzyl alcohol + CO₂ + glycine  
**Other name(s):** benzyloxy carbonylglycine hydrolase; N'-carbobenzoxy amino acid amidohydrolase; N'-benzyloxy carbonyl amino acid urethane hydrolase; N'-benzyloxycarbonyl amino acid urethane hydrolase I  
**Systematic name:** N-benzyloxy carbonylglycine urethane hydrolase  
**Comments:** Also acts, more slowly, on N-benzyloxy carbonylalanine, but not on the corresponding derivatives of other amino acids or on N-benzyloxy carbonylpeptides. Requires Co²⁺ or Zn²⁺. cf. EC 3.5.1.64, N'-benzyloxycarbonylleucine hydrolase.  
**References:** [1736]

[EC 3.5.1.58 created 1989]

EC 3.5.1.59

**Accepted name:** N-carbamoylsarcosine amidase  
**Reaction:** N-carbamoylsarcosine + H₂O = sarcosine + CO₂ + NH₃  
**Other name(s):** carbamoylsarcosine amidase  
**Systematic name:** N-carbamoylsarcosine amidohydrolase  
**References:** [508]

[EC 3.5.1.59 created 1989]

EC 3.5.1.60

**Accepted name:** N-(long-chain-acyl)ethanolamine deacylase  
**Reaction:** N-(long-chain-acyl)ethanolamine + H₂O = a long-chain carboxylate + ethanolamine  
**Other name(s):** N-acylethanolamine amidohydrolase; acylethanolamine amidase  
**Systematic name:** N-(long-chain-acyl)ethanolamine amidohydrolase
Comments: Does not act on N-acylsphingosine or N,O-diacylethanolamine.
References: [2246]

[EC 3.5.1.60 created 1989]

EC 3.5.1.61
Accepted name: mimosinase
Reaction: \((S)-2\text{-amino-3-(3-hydroxy-4-oxo-4H-pyridin-1-yl)propanoate} + \text{H}_2\text{O} = 3\text{-hydroxy-4H-pyrid-4-one} + \text{L-serine}\)
Systematic name: mimosine amidohydrolase
Comments: An enzyme from *Leucaena leucocephala* leaf, which also contains the toxic amino acid, mimosine.
References: [2522]

[EC 3.5.1.61 created 1989]

EC 3.5.1.62
Accepted name: acetylputrescine deacetylase
Reaction: \(N\text{-acetylputrescine} + \text{H}_2\text{O} = \text{acetate} + \text{putrescine}\)
Systematic name: \(N\text{-acetylputrescine acetylhydrolase}\)
Comments: The enzyme from *Micrococcus luteus* also acts on \(N^8\text{-acetylspermidine}\) and \(\text{acetylcadaverine}\), but more slowly.
References: [2462]

[EC 3.5.1.62 created 1989]

EC 3.5.1.63
Accepted name: 4-acetamidobutyrate deacetylase
Reaction: \(4\text{-acetamidobutanoate} + \text{H}_2\text{O} = \text{acetate} + 4\text{-aminobutanoate}\)
Systematic name: 4-acetamidobutanoate amidohydrolase
Comments: Also acts on \(N\text{-acetyl-}\beta\text{-alanine}\) and \(5\text{-acetamidopentanoate}\).
References: [964]

[EC 3.5.1.63 created 1989]

EC 3.5.1.64
Accepted name: \(N^\alpha\text{-benzyloxy carbonylL-leucine hydrolase}\)
Reaction: \(N^\alpha\text{-benzyloxy carbonylL-leucine} + \text{H}_2\text{O} = \text{benzyl alcohol} + \text{CO}_2 + \text{L-leucine}\)
Other name(s): benzylxocarbonylleucine hydrolase; \(N^\alpha\text{-benzyloxy carbonyl amino acid urethane hydrolase IV}; \alpha\text{-N-benzyloxy carbonylL-leucine urethane hydrolase}\)
Systematic name: \(N^\alpha\text{-benzyloxy carbonylL-leucine urethane hydrolase}\)
Comments: Also acts on \(N^\alpha\text{-t-butoxy carbonylL-leucine}\), and, more slowly, on the corresponding derivatives of \(\text{L-aspartate, L-methionine, L-glutamate and L-alanine}\). cf. EC 3.5.1.58 \(N\text{-benzyloxy carbonylglycine hydrolase}\).
References: [1591]

[EC 3.5.1.64 created 1989]

EC 3.5.1.65
Accepted name: theanine hydrolase
Reaction: \(N^3\text{-ethylL-glutamine} + \text{H}_2\text{O} = \text{L-glutamate} + \text{ethylamine}\)
Other name(s): L-theanine amidohydrolase; \(5\text{-N-ethylL-glutamine amidohydrolase}\)
Systematic name: \(N^3\text{-ethylL-glutamine amidohydrolase}\)
Comments: Also acts on other N-alkyl-L-glutamines.
References: [2619]

[EC 3.5.1.65 created 1989]

**EC 3.5.1.66**

**Accepted name:** 2-(hydroxymethyl)-3-(acetamidomethylene)succinate hydrolase  
**Reaction:** 2-(hydroxymethyl)-3-(acetamidomethylene)succinate + 2 H₂O = acetate + 2-(hydroxymethyl)-4-oxobutanoate + NH₃ + CO₂  
**Other name(s):** compound B hydrolase; α-hydroxymethyl-α’-(N-acetylaminomethylene)succinic acid hydrolase  
**Systematic name:** 2-(hydroxymethyl)-3-(acetamidomethylene)succinate amidohydrolase (deaminating, decarboxylating)  
**Comments:** Involved in the degradation of pyridoxin by *Pseudomonas* and *Arthrobacter*.  
**References:** [1064]

[EC 3.5.1.66 created 1989]

**EC 3.5.1.67**

**Accepted name:** 4-methyleneglutaminase  
**Reaction:** 4-methylene-L-glutamine + H₂O = 4-methylene-L-glutamate + NH₃  
**Other name(s):** 4-methyleneglutamine deamidase; 4-methyleneglutamine amidohydrolase  
**Systematic name:** 4-methylene-L-glutamine amidohydrolase  
**References:** [1068]

[EC 3.5.1.67 created 1989]

**EC 3.5.1.68**

**Accepted name:** N-formylglutamate deformylase  
**Reaction:** N-formyl-L-glutamate + H₂O = formate + L-glutamate  
**Other name(s):** β-citryl-L-glutamate hydrolase; formylglutamate deformylase; N-formylglutamate hydrolase; β-citrylglutamate amidase; β-citryl-L-glutamate amidohydrolase; β-citrylglutamate amidase; β-citryl-L-glutamate-hydrolyzing enzyme  
**Systematic name:** N-formyl-L-glutamate amidohydrolase  
**Comments:** The animal enzyme also acts on β-citryl-L-glutamate and β-citryl-L-glutamine.  
**References:** [1053, 1680]

[EC 3.5.1.68 created 1989]

**EC 3.5.1.69**

**Accepted name:** glycosphingolipid deacylase  
**Reaction:** Hydrolysis of gangliosides and neutral glycosphingolipids, releasing fatty acids to form the lyso-derivatives  
**Other name(s):** glycosphingolipid ceramide deacylase  
**Systematic name:** glycosphingolipid amidohydrolase  
**Comments:** Does not act on sphingolipids such as ceramide. Not identical with EC 3.5.1.23 ceramidase.  
**References:** [1009]

[EC 3.5.1.69 created 1990]

**EC 3.5.1.70**

**Accepted name:** aculeacin-A deacylase  
**Reaction:** Hydrolysis of the amide bond in aculeacin A and related neutral lipopeptide antibiotics, releasing the long-chain fatty acid side-chain
Other name(s): aculeacin A acylase
Systematic name: aculeacin-A amidohydrolase
References: [2501]

[EC 3.5.1.70 created 1992]

EC 3.5.1.71
Accepted name: N-feruloylglycine deacylase
Reaction: N-feruloylglycine + H₂O = ferulate + glycine
Other name(s): N-feruloylglycine hydrolase
Systematic name: N-feruloylglycine amidohydrolase
Comments: Hydrolyses a range of L-amino acids from the cinnamoyl and substituted cinnamoyl series. Not identical with EC 3.5.1.14 aminoacylase.
References: [1571, 1570]

[EC 3.5.1.71 created 1992]

EC 3.5.1.72
Accepted name: D-benzoylarginine-4-nitroanilide amidase
Reaction: N-benzoyl-D-arginine-4-nitroanilide + H₂O = N-benzoyl-D-arginine + 4-nitroaniline
Other name(s): benzoyl-D-arginine arylamidase; D-BAPA-ase
Systematic name: N-benzoyl-D-arginine-4-nitroanilide amidohydrolase
References: [834]

[EC 3.5.1.72 created 1992]

EC 3.5.1.73
Accepted name: carnitinamidase
Reaction: L-carnitinamide + H₂O = L-carnitine + NH₃
Other name(s): L-carnitinamidase; carnitine amidase; L-carnitine amidase
Systematic name: L-carnitinamide amidohydrolase
Comments: Does not act on D-carnitinamide.
References: [1777]

[EC 3.5.1.73 created 1992]

EC 3.5.1.74
Accepted name: chenodeoxycholoyltaurine hydrolase
Reaction: chenodeoxycholoyltaurine + H₂O = chenodeoxycholate + taurine
Systematic name: chenodeoxycholoyltaurine amidohydrolase
Comments: Some other taurine conjugates are hydrolysed, but not glycine conjugates of bile acids.
References: [1218]

[EC 3.5.1.74 created 1992]

EC 3.5.1.75
Accepted name: urethanase
Reaction: urethane + H₂O = ethanol + CO₂ + NH₃
Other name(s): urethane hydrolase
Systematic name: urethane amidohydrolase (decarboxylating)
References: [1288]
EC 3.5.1.76

Accepted name: arylalkyl acylamidase
Reaction: \( \text{N-acetylarylalkylamine} + \text{H}_2\text{O} = \text{arylalkylamine} + \text{acetate} \)
Other name(s): aralkyl acylamidase
Systematic name: \( \text{N-acetylarylalkylamine amidohydrolase} \)
Comments: Identified in \textit{Pseudomonas putida}. Strict specificity for \( \text{N-} \)acetyl arylalkylamines, including \( \text{N-} \)acetyl-2-phenylethylamine, \( \text{N-} \)acetyl-3-phenylpropylamine, \( \text{N-} \)acetyl-dopamine, \( \text{N-} \)acetyl-serotonin and melatonin. It also accepts arylalkyl acetates but not acetanilide derivatives, which are common substrates of EC 3.5.1.13, aryl acylamidase.

References: [2304]

EC 3.5.1.77

Accepted name: \( \text{N-} \)carbamoyl-\text{D}-amino-acid hydrolase
Reaction: \( \text{an \( \text{N-} \)carbamoyl-\text{D}-amino acid} + \text{H}_2\text{O} = \text{a \text{D}-amino acid} + \text{NH}_3 + \text{CO}_2 \)
Other name(s): \( \text{D-}\text{N-} \)carbamoylase; \( \text{N-} \)carbamoylase (ambiguous); \( \text{N-} \)carbamoyl-\text{D}-amino acid hydrolase
Systematic name: \( \text{N-} \)carbamoyl-\text{D}-amino-acid amidohydrolase
Comments: This enzyme, along with EC 3.5.1.87 (\( \text{N-} \)carbamoyl-\text{L}-amino-acid hydrolase), EC 5.1.99.5 (hydantoin racemase) and hydantoinase, forms part of the reaction cascade known as the "hydantoinase process", which allows the total conversion of \( \text{D, L-5-monosubstituted hydantoins} \) into optically pure \( \text{D-} \)or \( \text{L-} \)amino acids [39]. It has strict stereospecificity for \( \text{N-} \)carbamoyl-\text{D}-amino acids and does not act upon the corresponding \( \text{L-} \)amino acids or on the \( \text{N-} \)formyl amino acids, \( \text{N-} \)carbamoyl-sarcosine, -citrulline, -allantoin and -ureidopropanoate, which are substrates for other amidohydrolases.

References: [1865, 39]

EC 3.5.1.78

Accepted name: glutathionylspermidine amidase
Reaction: \( \text{glutathionylspermidine} + \text{H}_2\text{O} = \text{glutathione} + \text{spermidine} \)
Other name(s): glutathionylspermidine amidohydrolase (spermidine-forming)
Systematic name: \( \gamma\text{-L-glutamyl-L-cysteinyl-glycine:spermidine amidase} \)
Comments: Spermidine is numbered so that atom \( \text{N}-1 \) is in the amino group of the aminopropyl part of the molecule. The enzyme from \textit{Escherichia coli} is bifunctional and also catalyses the glutathionylspermidine synthase (EC 6.3.1.8) reaction, resulting in a net hydrolysis of ATP.

References: [234]

EC 3.5.1.79

Accepted name: phthalyl amidase
Reaction: \( \text{a phthalylamide} + \text{H}_2\text{O} = \text{phthalic acid} + \text{a substituted amine} \)
Systematic name: \( \text{phthalyl-amide amidohydrolase} \)
Comments: In the entry, "phthalyl" is used to mean "2-carboxybenzoyl". The enzyme from \textit{Xanthobacter agilis} hydrolyses phthalylated amino acids, peptides, \( \beta \)-lactams, aromatic and aliphatic amines. The substituent on nitrogen may be an alkyl group, but may also be complex, giving an amino acid or peptide derivative. Substitutions on the phthalyl ring include 6-F, 6-NH\textsubscript{2}, 3-OH, and a nitrogen in the aromatic ring \textit{ortho} to the carboxy group attached to the amine. No cofactors are required.

References: [268, 208, 443, 267]
EC 3.5.1.81
Accepted name: N-acyl-D-amino-acid deacylase
Reaction: N-acyl-D-amino acid + H₂O = an acid + D-amino acid
Systematic name: N-acyl-D-amino acid amidohydrolase
Comments: The enzyme from Alcaligenes denitrificans subsp. xylosoxydans and Alcaligenes xylosoxydans subsp. xylosoxydans has wide specificity; hydrolyses N-acyl derivative of neutral D-amino acids. Used in separating D- and L-amino acids. Requires zinc.
References: [2715, 2714]

EC 3.5.1.82
Accepted name: N-acyl-D-glutamate deacylase
Reaction: N-acyl-D-glutamate + H₂O = a carboxylate + D-glutamate
Systematic name: N-acyl-D-glutamate amidohydrolase
Comments: The enzyme from Alcaligenes xylosoxydans subsp. xylosoxydans and Pseudomonas sp. is specific for N-acyl-D-glutamate. Requires zinc.
References: [2713, 2716, 2717]

EC 3.5.1.83
Accepted name: N-acyl-D-aspartate deacylase
Reaction: N-acyl-D-aspartate + H₂O = a carboxylate + D-aspartate
Systematic name: N-acyl-D-aspartate amidohydrolase
Comments: The enzyme from Alcaligenes xylosoxydans subsp. xylosoxydans is specific for N-acyl-D-aspartate. Requires zinc.
References: [1703, 2718]

EC 3.5.1.84
Accepted name: biuret amidohydrolase
Reaction: biuret + H₂O = urea-1-carboxylate + NH₃
Systematic name: biuret amidohydrolase
Comments: Along with EC 3.5.2.15 (cyanuric acid amidohydrolase) and EC 3.5.1.54 (allophanate hydrolase), this enzyme forms part of the cyanuric-acid metabolism pathway, which degrades s-triazide herbicides, such as atrazine [2-chloro-4-(ethylamino)-6-(isopropylamino)-1,3,5-triazine], in bacteria. Urea-1-carboxylate rather than urea (as was thought previously) is the 2-nitrogen intermediate in cyanuric-acid metabolism in bacteria [383]. The product, urea-1-carboxylate, can spontaneously decarboxylate under acidic conditions to form urea but, under physiological conditions, it can be converted into CO₂ and ammonia by the action of EC 3.5.1.54 [383].
References: [435, 383, 2288]
EC 3.5.1.85
Accepted name: (S)-N-acetyl-1-phenylethylamine hydrolase
Reaction: N-acetylphenylethylamine + H₂O = phenylethylamine + acetate
Systematic name: (S)-N-acetylphenylethylamine: H₂O hydrolase
Comments: Inhibited by phenylmethanesulfonyl fluoride. Some related acetylated compounds are hydrolysed with variable enantiomeric selectivities.
References: [294]

[EC 3.5.1.85 created 2000, modified 2002]

EC 3.5.1.86
Accepted name: mandelamid amidase
Reaction: (R)-mandelamide + H₂O = (R)-mandelate + NH₃
Other name(s): Pseudomonas mandelamide hydrolase
Systematic name: mandelamide hydrolase
References: [2848]

[EC 3.5.1.86 created 2000]

EC 3.5.1.87
Accepted name: N-carbamoyl-L-amino-acid hydrolase
Reaction: an N-carbamoyl-L-2-amino acid (a 2-ureido carboxylate) + H₂O = an L-2-amino acid + NH₃ + CO₂
Other name(s): N-carbamyl L-amino acid amidohydrolase; N-carbamoyl-L-amino acid amidohydrolase; L-N-carbamoylase; N-carbamoylase (ambiguous)
Systematic name: N-carbamoyl-L-amino-acid amidohydrolase
Comments: This enzyme, along with EC 3.5.1.77 (N-carbamoyl-D-amino-acid hydrolase), EC 5.1.99.5 (hydrantoin racemase) and hydantoinase, forms part of the reaction cascade known as the "hydrantoinase process", which allows the total conversion of D,L-5-monosubstituted hydantoins into optically pure D- or L-amino acids [39]. The enzyme from Alcaligenes xylosoxidans has broad specificity for carbamoyl-L-amino acids, although it is inactive on the carbamoyl derivatives of glutamate, aspartate, arginine, tyrosine or tryptophan. The enzyme from Sinorhizobium meliloti requires a divalent cation for activity and can hydrolyse N-carbamoyl-L-tryptophan as well as N-carbamoyl L-amino acids with aliphatic substituents [1577]. The enzyme is inactive on derivatives of D-amino acids. In addition to N-carbamoyl L-amino acids, the enzyme can also hydrolyse formyl and acetyl derivatives to varying degrees [1864, 1577].
References: [1864, 1577, 39]

[EC 3.5.1.87 created 2001, modified 2008]

EC 3.5.1.88
Accepted name: peptide deformylase
Reaction: formyl-L-methionyl peptide + H₂O = formate + methionyl peptide
Systematic name: formyl-L-methionyl peptide amidohydrolase
Comments: Requires Fe(II). Also requires at least a dipeptide for an efficient rate of reaction. N-terminal L-methionine is a prerequisite for activity but the enzyme has broad specificity at other positions. Differs in substrate specificity from EC 3.5.1.27 (N-formylmethionylaminoacyl-tRNA deformylase) and EC 3.5.1.31 (formylmethionine deformylase).
References: [16, 1606, 356, 163, 162, 2046, 876, 2045, 1054, 2042, 813, 1955]

[EC 3.5.1.88 created 2001]

EC 3.5.1.89
Accepted name: N-acetylglucosaminylphosphatidylinositol deacytylease
Reaction: \[ 6-(\text{N-acetyl-}\alpha\text{-d-glucosaminyl})-1\text{-phosphatidyl-1-d-my o-inositol} + \text{H}_2\text{O} = 6-(\alpha\text{-d-glucosaminyl})-1\text{-phosphatidyl-1-d-my o-inositol} + \text{acetate} \]

Other name(s): 
- N-acetyl-d-glucosaminylphosphatidylinositol acetylhydrolase; 
- N-acetylglucosaminylphosphatidylinositol de-N-acetylase; 
- GlcNAc-PI de-N-acetylase; 
- acetylglucosaminylphosphatidylinositol deacetylase

Systematic name: 6-(N-acetyl-\alpha\text{-d-glucosaminyl})-1-phosphatidyl-1\text{-d-my o-inositol acetylhydrolase}

Comments: Involved in the second step of glycosylphosphatidylinositol (GPI) anchor formation in all eukaryotes. The enzyme appears to be composed of a single subunit (PIG-L in mammalian cells and GPI12 in yeast). In some species, the long-chain sn-1-acyl group of the phosphatidyl group is replaced by a long-chain alkyl or alk-1-enyl group.

References: [557, 1774, 2751, 2371]

[EC 3.5.1.89 created 1992 as EC 3.1.1.69, transferred 2002 to EC 3.5.1.89, modified 2002]

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EC 3.5.1.90

Accepted name: adenosylcobinamide hydrolase

Reaction: \[ \text{adenosylcobinamide} + \text{H}_2\text{O} = \text{adenosylcobyric acid} + (\text{R})\text{-1-aminopropan-2-ol} \]

Other name(s): CbiZ; AdoCbi amidohydrolase

Systematic name: adenosylcobinamide amidohydrolase

Comments: Involved in the salvage pathway of cobinamide in archaea. \textit{Archaea} convert adenosylcobinamide (AdoCbi) into adenosylcobinamide phosphate (AdoCbi-P) in two steps. First, the amidohydrolase activity of CbiZ cleaves off the aminopropanol moiety of AdoCbi yielding adenosylcobyric acid (AdoCby); second, AdoCby is converted into AdoCbi-P by the action of EC 6.3.1.10, adenosylcobinamide-phosphate synthase (CbiB).

References: [2824]

[EC 3.5.1.90 created 2004]

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EC 3.5.1.91

Accepted name: \(N\)-substituted formamide deformylase

Reaction: \[ \text{N-benzylformamide} + \text{H}_2\text{O} = \text{formate} + \text{benzylamine} \]

Other name(s): NfdA

Systematic name: \(N\)-benzylformamide amidohydrolase

Comments: Zinc is a cofactor. While \(N\)-benzylformamide is the best substrate, the enzyme from \textit{Arthrobacter pascens} can also act on the \(N\)-substituted formamides \(N\)-butylformamide, \(N\)-allylformamide, \(N\)-[2-(cyclohex-1-enyl)ethyl]formamide and \(N\)-(1-phenylethyl)formamide, but much more slowly. Amides of other acids do not act as substrates.

References: [761]

[EC 3.5.1.91 created 2005]

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EC 3.5.1.92

Accepted name: pantetheine hydrolase

Reaction: \[ (\text{R})\text{-pantetheine} + \text{H}_2\text{O} = (\text{R})\text{-pantothenate} + 2\text{-aminoethanethiol} \]

Other name(s): pantetheinase; vanin; vanin-1

Systematic name: \(\text{(R)}\text{-pantetheine amidohydrolase} \)

Comments: The enzyme hydrolyses only one of the amide bonds of pantetheine. The substrate analogues phosphopantetheine and CoA are not substrates. The enzyme recycles pantothenate (vitamin \(B_5\)) and produces 2-aminoethanethiol (cysteamine), a potent anti-oxidant [1985].

References: [598, 599, 1559, 89, 1985, 1572, 1925]

[EC 3.5.1.92 created 2006]
EC 3.5.1.93
Accepted name: glutaryl-7-aminocephalosporanic-acid acylase
Reaction: (7R)-7-(4-carboxybutanamido)cephalosporanate + H₂O = (7R)-7-aminocephalosporanate + glutarate
Other name(s): 7β-(4-carboxybutanamido)cephalosporanic acid acylase; cephalosporin C acylase; glutaryl-7-ACA acylase; CA; GCA; GA; cephalosporin acylase; glutaryl-7-aminocephalosporanic acid acylase; GL-7-ACA acylase
Systematic name: (7R)-7-(4-carboxybutanamido)cephalosporanate amidohydrolase
Comments: Forms 7-aminocephalosporanic acid, a key intermediate in the synthesis of cephem antibiotics. It reacts only weakly with cephalosporin C.
References: [1099, 1269, 1697, 1368, 1264, 1057, 1259]

[EC 3.5.1.93 created 2005]

EC 3.5.1.94
Accepted name: γ-glutamyl-γ-aminobutyrate hydrolase
Reaction: 4-(glutamylamino)butanoate + H₂O = 4-aminobutanoate + L-glutamate
Other name(s): γ-glutamyl-GABA hydrolase; PuuD; YcjL; 4-(γ-glutamylamino)butanoate amidohydrolase
Systematic name: 4-(glutamylamino)butanoate amidohydrolase
Comments: Forms part of a novel putrescine-utilizing pathway in Escherichia coli, in which it has been hypothesized that putrescine is first glutamylated to form γ-glutamylputrescine, which is oxidized to 4-(γ-glutamylamino)butanal and then to 4-(γ-glutamylamino)butanoate. The enzyme can also catalyse the reactions of EC 3.5.1.35 (D-glutaminase) and EC 3.5.1.65 (theanine hydrolase).
References: [1356]

[EC 3.5.1.94 created 2006]

EC 3.5.1.95
Accepted name: N-malonylurea hydrolase
Reaction: 3-oxo-3-ureidopropanoate + H₂O = malonate + urea
Other name(s): ureidomalonase
Systematic name: 3-oxo-3-ureidopropanoate amidohydrolase (urea- and malonate-forming)
Comments: Forms part of the oxidative pyrimidine-degrading pathway in some microorganisms, along with EC 1.17.99.4 (uracil/thymine dehydrogenase) and EC 3.5.2.1 (barbiturase).
References: [2389, 2388]

[EC 3.5.1.95 created 2006]

EC 3.5.1.96
Accepted name: succinylglutamate desuccinylase
Reaction: N-succinyl-L-glutamate + H₂O = succinate + L-glutamate
Other name(s): N²-succinylglutamate desuccinylase; SGDS; AstE
Systematic name: N-succinyl-L-glutamate amidohydrolase
Comments: Requires Co²⁺ for maximal activity [2757]. N²-Acetylglutamate is not a substrate. This is the final enzyme in the arginine succinyltransferase (AST) pathway for the catabolism of arginine [2757]. 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).
References: [2757, 463, 464, 1105, 2251]

[EC 3.5.1.96 created 2006]
EC 3.5.1.97

**Accepted name:** acyl-homoserine-lactone acylase  
**Reaction:** an N-acyl-L-homoserine lactone + H₂O = L-homoserine lactone + a carboxylate  
**Other name(s):** acyl-homoserine lactone acylase; AHL-acylase; AiiD; N-acyl-homoserine lactone acylase; PA2385 protein; quorum-quenching AHL acylase; quorum-quenching enzyme; PvdQ; QuiP  
**Systematic name:** N-acyl-L-homoserine-lactone amidohydrolase  
**Comments:** Acyl-homoserine lactones (AHLs) are produced by a number of bacterial species and are used by them to regulate the expression of virulence genes in a process known as quorum-sensing. Each bacterial cell has a basal level of AHL and, once the population density reaches a critical level, it triggers AHL-signalling which, in turn, initiates the expression of particular virulence genes. Plants or animals capable of degrading AHLs would have a therapeutic advantage in avoiding bacterial infection as they could prevent AHL-signalling and the expression of virulence genes in quorum-sensing bacteria. This quorum-quenching enzyme removes the fatty-acid side chain from the homoserine lactone ring of AHL-dependent quorum-sensing signal molecules [2341]. It has broad specificity for AHLs with side chains ranging in length from 11 to 14 carbons. Substituents at the 3′-position, as found in N-(3-oxododecanoyl)-L-homoserine lactone, do not affect this activity [2341].  
**References:** [2341, 1468]

[EC 3.5.1.97 created 2007]

EC 3.5.1.98

**Accepted name:** histone deacetylase  
**Reaction:** Hydrolysis of an N⁶-acetyl-lysine residue of a histone to yield a deacetylated histone  
**Other name(s):** HDAC  
**Systematic name:** histone amidohydrolase  
**Comments:** A class of enzymes that remove acetyl groups from N⁶-acetyl-lysine residues on a histone. The reaction of this enzyme is opposite to that of EC 2.3.1.48, histone acetyltransferase. Histone deacetylases (HDACs) can be organized into three classes, HDAC1, HDAC2 and HDAC3, depending on sequence similarity and domain organization. Histone acetylation plays an important role in regulation of gene expression. In eukaryotes, HDACs play a key role in the regulation of transcription and cell proliferation [2386]. May be identical to EC 3.5.1.17, acyl-lysine deacylase.  
**References:** [1330, 512, 1922, 2386, 688, 1972, 500]

[EC 3.5.1.98 created 2008]

EC 3.5.1.99

**Accepted name:** fatty acid amide hydrolase  
**Reaction:** (1) anandamide + H₂O = arachidonic acid + ethanolamine  
(2) oleamide + H₂O = oleic acid + NH₃  
**Other name(s):** FAAH; oleamide hydrolase; anandamide amidohydrolase  
**Systematic name:** fatty acylamide amidohydrolase  
**Comments:** Integral membrane protein, the enzyme is responsible for the catabolism of neuromodulatory fatty acid amides, including anandamide and oleamide, occurs in mammalia.  
**References:** [230, 1945, 1944]

[EC 3.5.1.99 created 2009]

EC 3.5.1.100

**Accepted name:** (R)-amidase  
**Reaction:** (1) (R)-piperazine-2-carboxamide + H₂O = (R)-piperazine-2-carboxylic acid + NH₃  
(2) β-alaninamide + H₂O = β-alanine + NH₃  
**Other name(s):** R-stereospecific amidase; R-amidase  
**Systematic name:** (R)-piperazine-2-carboxamide amidohydrolase

[240]
In addition \((R)\)-piperidine-3-carboxamide is hydrolysed to \((R)\)-piperidine-3-carboxylic acid and \(\text{NH}_3\), and \((R)\)-piperazine-2-\text{tert}-butylcarboxamide is hydrolysed to \((R)\)-piperazine-2-\text{tert}-butylcarboxylic acid and \(\text{NH}_3\) with lower activity. The enzyme does not act on the other amide substrates for EC 3.5.1.4 (amidase).

**References:** [1302]

**EC 3.5.1.101**

**Accepted name:** l-proline amide hydrolase

**Reaction:**
1. \((S)\)-piperidine-2-carboxamide + \(\text{H}_2\text{O}\) = \((S)\)-piperidine-2-carboxylic acid + \(\text{NH}_3\)
2. \(l\)-prolinamide + \(\text{H}_2\text{O}\) = \(l\)-proline + \(\text{NH}_3\)

**Other name(s):** \(S\)-stereoselective piperazine-2-\text{tert}-butylcarboxamide hydrolase; LaaA; \(l\)-amino acid amidase

**Systematic name:** \((S)\)-piperidine-2-carboxamide amidohydrolase

**References:** [1303]

**EC 3.5.1.102**

**Accepted name:** 2-amino-5-formylamino-6-\text{D-ribosylamino}pyrimidin-4(3\text{H})-one 5\text{'-monophosphate deformylase

**Reaction:**
2-amino-5-formylamino-6-\(\text{D-ribosylamino}\)pyrimidin-4(3\text{H})-one 5\text{'-phosphate + \(\text{H}_2\text{O}\) = 2,5-diamino-6-\(\text{D-ribosylamino}\)pyrimidin-4(3\text{H})-one 5\text{'-phosphate + formate

**Other name(s):** ArfB

**Systematic name:** 2-amino-5-formylamino-6-\(\text{D-ribosylamino}\)pyrimidin-4(3\text{H})-one 5\text{'-phosphate amidohydrolase

**Comments:**
The enzyme catalyses the second step in archaeal riboflavin and 7,8-didemethyl-8-hydroxy-5-deazariboflavin biosynthesis. The first step is catalysed by EC 3.5.4.29 (GTP cyclohydrolase IIa). The bacterial enzyme, EC 3.5.4.25 (GTP cyclohydrolase II) catalyses both reactions.

**References:** [877]

**EC 3.5.1.103**

**Accepted name:** \(N\)-acetyl-1-\text{D}-\text{myo}-inositol-2-amino-2-deoxy-\text{\textalpha-\textD-glucopyranoside} deacetylase

**Reaction:**
1-(2-acetamido-2-deoxy-\text{\textalpha-\textD-glucopyranosyl})-1\text{D}-\text{myo}-inositol + \(\text{H}_2\text{O}\) = 1-(2-amino-2-deoxy-\text{\textalpha-\textD-glucopyranoside})-1\text{D}-\text{myo}-inositol + acetate

**Other name(s):** MshB

**Systematic name:** 1-(2-acetamido-2-deoxy-\text{\textalpha-\textD-glucopyranosyl})-1\text{D}-\text{myo}-inositol acetylhydrolase

**Comments:**
This enzyme is considered the key enzyme and rate limiting step in the mycothiol biosynthesis pathway [2067]. In addition to acetylase activity, the enzyme possesses weak mycothiol conjugate amidase activity, and shares sequence similarity with mycothiol \(S\)-conjugate amidase [1800]. The enzyme requires a divalent transition metal ion for activity, believed to be \(\text{Zn}^{2+}\) [1605].

**References:** [2067, 1800, 1605]

**EC 3.5.1.104**

**Accepted name:** peptidoglycan-\(N\)-acetylglucosamine deacetylase

**Reaction:**
peptidoglycan-\(N\)-acetyl-\text{\textalpha-\textD-glucosamine} + \(\text{H}_2\text{O}\) = peptidoglycan-\(\text{\textalpha-\textD-glucosamine}\) + acetate

**Other name(s):** HP310; PgdA; SpPgdA; BC1960; peptidoglycan deacetylase; \(N\)-acetylglucosamine deacetylase; peptidoglycan \text{GlcNAc} deacetylase; peptidoglycan \(N\)-acetylglucosamine deacetylase; \(PG\) \(N\)-deacetylase

**Systematic name:** peptidoglycan-\(N\)-acetylglucosamine amidohydrolase

**References:** [2067, 1800, 1605]
Modification of peptidoglycan by \(N\)-deacetylation is an important factor in virulence of *Helicobacter pylori*, *Listeria monocytogenes* and *Streptococcus suis* [2731, 2006, 696]. The enzyme from *Streptococcus pneumoniae* is a metalloenzyme using a His-His-Asp zinc-binding triad with a nearby aspartic acid and histidine acting as the catalytic base and acid, respectively [212].

References: [2021, 2600, 212, 2731, 2006, 696]

[EC 3.5.1.104 created 2010]

**EC 3.5.1.105**

**Accepted name:** chitin disaccharide deacetylase

**Reaction:** 2-(acetylamino)-4-O-[2-(acetylamino)-2-deoxy-\(\beta\)-D-glucopyranosyl]-2-deoxy-\(\beta\)-D-glucopyranose + \(\text{H}_2\text{O}\) = 2-(acetylamino)-4-O-(2-amino-2-deoxy-\(\beta\)-D-glucopyranosyl)-2-deoxy-\(\beta\)-D-glucopyranose + acetate

**Other name(s):** chitobiose amidohydrolase; COD; chitin oligosaccharide deacetylase; chitin oligosaccharide amidohydrolase

**Systematic name:** 2-(acetylamino)-4-O-[2-(acetylamino)-2-deoxy-\(\beta\)-D-glucopyranosyl]-2-deoxy-\(\beta\)-D-glucopyranose acetylhydrolase

**Comments:** Chitin oligosaccharide deacetylase is a key enzyme in the chitin catabolic cascade of chitinolytic *Vibrio* strains. Besides being a nutrient, the heterodisaccharide product 4-O-(\(N\)-acetyl-\(\beta\)-D-glucosaminyl)-D-glucosamine is a unique inducer of chitinase production in *Vibrio parahaemolyticus* [1012]. In contrast to EC 3.5.1.41 (chitin deacetylase) this enzyme is specific for the chitin disaccharide [1173, 1875]. It also deacetylates the chitin trisaccharide with lower efficiency [1875]. No activity with higher polymers of GlcNAc [1173, 1875].

References: [1173, 1012, 1875, 1874]

[EC 3.5.1.105 created 2010]

**EC 3.5.1.106**

**Accepted name:** \(N\)-formylmaleamate deformylase

**Reaction:** \(N\)-formylmaleamic acid + \(\text{H}_2\text{O}\) = maleamate + formate

**Other name(s):** NicD

**Systematic name:** \(N\)-formylmaleamic acid amidohydrolase

**Comments:** The reaction is involved in the aerobic catabolism of nicotinic acid.

References: [1144]

[EC 3.5.1.106 created 2010]

**EC 3.5.1.107**

**Accepted name:** maleamate amidohydrolase

**Reaction:** maleamate + \(\text{H}_2\text{O}\) = maleate + \(\text{NH}_3\)

**Other name(s):** NicF

**Systematic name:** maleamate amidohydrolase

**Comments:** The reaction is involved in the aerobic catabolism of nicotinic acid.

References: [1144]

[EC 3.5.1.107 created 2010]

**EC 3.5.1.108**

**Accepted name:** UDP-3-O-acyl-\(N\)-acetylglucosamine deacetylase

**Reaction:** UDP-3-O-[(3\(R\))-3-hydroxymyristoyl]-\(N\)-acetylglucosamine + \(\text{H}_2\text{O}\) = UDP-3-O-[(3\(R\))-3-hydroxymyristoyl]-\(D\)-glucosamine + acetate

References: [2021, 2600, 212, 2731, 2006, 696]
Other name(s): LpxC protein; LpxC enzyme; LpxC deacetylase; deacetylase LpxC; UDP-3-O-acyl-GlcNAc deacetylase; UDP-3-O-((R)-3-hydroxymyristoyl)-N-acetylglucosamine deacetylase; UDP-(3-O-acyl)-N-acetylglucosamine deacetylase; UDP-3-O-(R-3-hydroxymyristoyl)-N-acetylglucosamine deacetylase; UDP-(3-O-(R-3-hydroxymyristoyl))-N-acetylglucosamine deacetylase

Systematic name: UDP-3-O-[(3R)-3-hydroxymyristoyl]-N-acetylglucosamine amidohydrolase

Comments: A zinc protein. The enzyme catalyses a committed step in the biosynthesis of lipid A.

References: [997, 1114, 1065, 2740, 2791, 1687]

EC 3.5.1.108 created 2010

EC 3.5.2 In cyclic amides

EC 3.5.2.1
Accepted name: barbiturase
Reaction: barbiturate + H₂O = 3-oxo-3-ureidopropanoate
Systematic name: barbiturate amidohydrolase (3-oxo-3-ureidopropanoate-forming)
Comments: Contains zinc and is specific for barbiturate as substrate [2388]. Forms part of the oxidative pyrimidine-degrading pathway in some microorganisms, along with EC 1.17.99.4 (uracil/thymine dehydrogenase) and EC 3.5.1.95 (N-malonylurea hydrolase). It was previously thought that the end-products of the reaction were malonate and urea but this has since been disproved [2389]. May be involved in the regulation of pyrimidine metabolism, along with EC 2.4.2.9, uracil phosphoribosyltransferase.
References: [957, 2389, 2388]

EC 3.5.2.2 created 1961, modified 2006

EC 3.5.2.2
Accepted name: dihydropyrimidinase
Reaction: 5,6-dihydropyrimidinase + H₂O = 3-ureidopropanoate
Other name(s): hydantoinase; hydropyrimidine hydrase; hydantoin peptidase; pyrimidine hydrase; D-hydantoinase
Systematic name: 5,6-dihydropyrimidine amidohydrolase
Comments: Also acts on dihydrothymine and hydantoin.
References: [282, 602]

EC 3.5.2.3 created 1961

EC 3.5.2.3
Accepted name: dihydroorotase
Reaction: (S)-dihydroorotate + H₂O = N-carbamoyl-L-aspartate
Other name(s): carbamoylaspartic dehydrase; dihydroorotate hydrolase
Systematic name: (S)-dihydroorotate amidohydrolase
References: [436, 1454]

EC 3.5.2.3 created 1961

EC 3.5.2.4
Accepted name: carboxymethylhydantoinase
Reaction: L-5-carboxymethylhydantoin + H₂O = N-carbamoyl-L-aspartate
Other name(s): hydantoin hydrolase
Systematic name: L-5-carboxymethylhydantoin amidohydrolase
References: [1454]
EC 3.5.2.5
Accepted name: allantoinase
Reaction: (S)-allantoin + H₂O → allantoate
Systematic name: (S)-allantoin amidohydrolase
References: [703]

[EC 3.5.2.5 created 1961]

EC 3.5.2.6
Accepted name: β-lactamase
Reaction: a β-lactam + H₂O → a substituted β-amino acid
Other name(s): penicillinas; cephalosporinase; neutrapen; penicillin β-lactamase; exopenicillinase; ampicillinase; penicillin amido-β-lactamhydrolylase; penicillinas I, II; β-lactamase I-III; β-lactamase A, B, C; β-lactamase AME I; cephalosporin-β-lactamase
Systematic name: β-lactam hydrolase
Comments: A group of enzymes of varying specificity hydrolysing β-lactams; some act more rapidly on penicillins, some more rapidly on cephalosporins. The latter were formerly listed as EC 3.5.2.8, cephalosporinase.
References: [408, 982, 1366, 2000, 2001, 2149]

[EC 3.5.2.6 created 1961, modified 1981 (EC 3.5.2.8 created 1972, incorporated 1978)]

EC 3.5.2.7
Accepted name: imidazolonepropionate
Reaction: (S)-3-(5-oxo-4,5-dihydro-3H-imidazol-4-yl)propanoate + H₂O → N-formimidoyl-L-glutamate + H⁺
Other name(s): 4(5)-imidazolone-5(4)-propionic acid hydrolase; imidazolone propionic acid hydrolase
Systematic name: 3-(5-oxo-4,5-dihydro-3H-imidazol-4-yl)propanoate amidohydrolase
References: [2059, 2374]

[EC 3.5.2.7 created 1965, modified 2001]

[3.5.2.8 Deleted entry. cephalosporinase. Now included with EC 3.5.2.6 β-lactamase]  
[EC 3.5.2.8 created 1972, deleted 1978]

EC 3.5.2.9
Accepted name: 5-oxoprolinase (ATP-hydrolysing)
Reaction: ATP + 5-oxo-L-proline + 2 H₂O → ADP + phosphate + L-glutamate
Other name(s): pyroglutamase (ATP-hydrolysing); oxoprolinase; pyroglutamase; 5-oxoprolinase; pyroglutamate hydrolylase; pyroglutamic hydrolylase; L-pyroglutamate hydrolylase; 5-oxo-L-prolinase; pyroglutamase
Systematic name: 5-oxo-L-proline amidohydrolase (ATP-hydrolysing)
References: [2674]

[EC 3.5.2.9 created 1976]

EC 3.5.2.10
Accepted name: creatininase
Reaction: creatinine + H₂O → creatine
Other name(s): creatinine hydrolylase
Systematic name: creatinine amidohydrolase
References: [2617]

[EC 3.5.2.10 created 1961]
EC 3.5.2.11

**Accepted name:** L-lysine-lactamase

**Reaction:** L-lysine 1,6-lactam + H₂O = L-lysine

**Other name(s):** L-lysine-1,6-lactam hydrolase; L-lysaminidase

**Systematic name:** L-lysine-1,6-lactam lactamhydrolase

**Comments:** Also hydrolyses L-lysinamide.

**References:** [765, 2317]

EC 3.5.2.12

**Accepted name:** 6-aminohexanoate-cyclic-dimer hydrolase

**Reaction:** 1,8-diazacyclotetradecane-2,9-dione + H₂O = N-(6-aminohexanoyl)-6-aminohexanoate

**Systematic name:** 1,8-diazacyclotetradecane-2,9-dione lactamhydrolase

**Comments:** The cyclic dimer of 6-aminohexanoate is converted to the linear dimer.

**References:** [1267]

EC 3.5.2.13

**Accepted name:** 2,5-dioxopiperazine hydrolase

**Reaction:** 2,5-dioxopiperazine + H₂O = glycylglycine

**Other name(s):** cyclo(Gly-Gly) hydrolase; cyclo(glycylglycine) hydrolase

**Systematic name:** 2,5-dioxopiperazine amidohydrolase

**Comments:** Highly specific; does not hydrolyse other dioxopiperazines, glycylglycine, proteins or barbiturates.

**References:** [2465]

EC 3.5.2.14

**Accepted name:** N-methylhydantoinase (ATP-hydrolysing)

**Reaction:** ATP + N-methylimidazolidine-2,4-dione + 2 H₂O = ADP + phosphate + N-carbamoylsarcosine

**Other name(s):** N-methylhydantoin amidohydrolase; methylhydantoin amidase; N-methylhydantoin hydrolase; N-methylhydantoinase

**Systematic name:** N-methylimidazolidine-2,4-dione amidohydrolase (ATP-hydrolysing)

**References:** [1261]

EC 3.5.2.15

**Accepted name:** cyanuric acid amidohydrolase

**Reaction:** cyanuric acid + H₂O = biuret + CO₂

**Other name(s):** AtzD

**Systematic name:** cyanuric acid amidohydrolase

**Comments:** Along with EC 3.5.1.54 (allophanate hydrolase) and EC 3.5.1.84 (biuret amidohydrolase), this enzyme forms part of the cyanuric-acid metabolism pathway, which degrades s-triazide herbicides, such as atrazine [2-chloro-4-(ethylamino)-6-(isopropylamino)-1,3,5-triazine], in bacteria. This is a key enzyme in the pathway, catalysing the ring cleavage of cyanuric acid. The enzyme is specific for cyanuric acid as substrate as neither the structurally related compounds ammeline (2,4-diamino-6-hydroxy-s-triazine) and ammelide (2-amino-4,6-dihydroxy-s-triazine) nor a number of pyrimidine compounds, such as uracil and cytosine, can act as substrates [1202].
EC 3.5.2.15
Accepted name: maleimide hydrolase
Reaction: maleimide + H$_2$O = maleamic acid
Other name(s): imidase; cyclic imide hydrolase; cyclic-imide amidohydrolase (decyclicizing) [misprint]
Systematic name: cyclic-imide amidohydrolase (decyclizing)
Comments: Succinimide and glutarimide, and sulfur-containing cyclic imides, such as rhodanine, can also act as substrates for the enzyme from Blastobacter sp. A17p-4. The reverse, cyclization, reaction is also catalysed, but much more slowly. It has lower activity towards cyclic ureides, which are the substrates of EC 3.5.2.2, dihydropyrimidinase.
References: [1866]

EC 3.5.2.16
Accepted name: hydroxyisourate hydrolase
Reaction: 5-hydroxyisourate + H$_2$O = 5-hydroxy-2-oxo-4-ureido-2,5-dihydro-1$H$-imidazole-5-carboxylate
Other name(s): HIUHase; 5-hydroxyisourate hydrolase
Systematic name: 5-hydroxyisourate amidohydrolase
Comments: The reaction is the first stage in the conversion of 5-hydroxyisourate into $S$-allantoin. This reaction will also occur spontaneously but more slowly.
References: [2073, 2072, 2209]

EC 3.5.2.17
Accepted name: enamidase
Reaction: 6-oxo-1,4,5,6-tetrahydronicotinate + 2 H$_2$O = 2-formylglutarate + NH$_3$
Systematic name: 6-oxo-1,4,5,6-tetrahydronicotinate amidohydrolase
Comments: Contains iron and Zn$^{2+}$. 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 1.1.1.291 (2-hydroxymethylglutarate dehydrogenase), EC 5.4.99.4 (2-methyleneglutarate mutase), EC 5.3.3.6 (methylitaconate $\Delta$-isomerase), EC 4.2.1.85 (dimethylmaleate hydratase) and EC 4.1.3.32 (2,3-dimethylmalate lyase).
References: [31]

EC 3.5.3 In linear amidines

EC 3.5.3.1
Accepted name: arginase
Reaction: L-arginine + H$_2$O = L-ornithine + urea
Other name(s): arginine amidinase; canavanase; L-arginase; arginine transamidinase
Systematic name: L-arginine amidinohydrolase
Comments: Also hydrolyses $\alpha$-$N$-substituted L-arginines and canavanine.
References: [99, 316, 594, 863, 864]

EC 3.5.2.18 created 2006

EC 3.5.2.17 created 2004

EC 3.5.2.16 created 2001

EC 3.5.2.15 created 2000, modified 2008
EC 3.5.3.2
Accepted name: guanidinoacetase
Reaction: guanidinoacetate + H₂O = glycine + urea
Other name(s): glycocynamine
Systematic name: guanidinoacetate amidinohydrolase
Comments: Requires Mn²⁺.
References: [2131, 2891]

[EC 3.5.3.2 created 1961]

EC 3.5.3.3
Accepted name: creatinase
Reaction: creatine + H₂O = sarcosine + urea
Systematic name: creatine amidinohydrolase
References: [2131, 2896]

[EC 3.5.3.3 created 1961]

EC 3.5.3.4
Accepted name: allantoicase
Reaction: allantoin + H₂O = (S)-ureidoglycolate + urea
Systematic name: allantoate amidinohydrolase
Comments: Also hydrolyses (R)-ureidoglycolate to glyoxylate and urea.
References: [703, 2595, 2668, 2170]

[EC 3.5.3.4 created 1961]

EC 3.5.3.5
Accepted name: formimidoylaspartate deiminase
Reaction: N-formimidoyl-L-aspartate + H₂O = N-formyl-L-aspartate + NH₃
Other name(s): formiminoaspartate deiminase
Systematic name: N-formimidoyl-L-aspartate iminohydrolase
References: [961]

[EC 3.5.3.5 created 1961, modified 2000]

EC 3.5.3.6
Accepted name: arginine deiminase
Reaction: L-arginine + H₂O = L-citrulline + NH₃
Other name(s): arginine dihydrolase; citrulline iminase; L-arginine deiminase
Systematic name: L-arginine iminohydrolase
Comments: Also acts on canavanine.
References: [1870, 1966, 2064]

[EC 3.5.3.6 created 1961]

EC 3.5.3.7
Accepted name: guanidinobutyrase
Reaction: 4-guanidinobutanoate + H₂O = 4-aminobutanoate + urea
Other name(s): γ-guanidobutyrase; 4-guanidinobutyrate amidinobutyrase; γ-guanidinobutyrate amidinohydrolase; G-Base; GBH; guanidinobutyrate ureahydrolase
Systematic name: 4-guanidinobutanoate amidinohydrolase

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Comments: Requires Mn\(^{2+}\). Also acts, very slowly, on 5-guanidinopentanoate and 6-guanidinohexanoate.
References: [1700, 2549, 2888, 2889]

[EC 3.5.3.7 created 1972]

**EC 3.5.3.8**

**Accepted name:** formimidoylglutamase

**Reaction:** \(N\)-formimidoyl-L-glutamate + H\(_2\)O = L-glutamate + formamide

**Other name(s):** formiminoglutamase; \(N\)-formiminoglutamate hydrolase; \(N\)-formimino-L-glutamate formiminohydrolase

**Systematic name:** \(N\)-formimidoyl-L-glutamate formimidoylhydrolase

**References:** [1189, 1509]

[EC 3.5.3.8 created 1972, modified 2000, modified 2001]

**EC 3.5.3.9**

**Accepted name:** allantoate deiminase

**Reaction:** allantoate + H\(_2\)O = (S)-ureidoglycine + NH\(_3\) + CO\(_2\)

**Other name(s):** allantoate amidohydrolase

**Systematic name:** allantoate amidinohydrolase (decarboxylating)

**Comments:** This enzyme is part of the ureide pathway, which permits certain organisms to recycle the nitrogen in purine compounds. This enzyme, which liberates ammonia from allantoate, is present in plants and bacteria. In plants it is localized in the endoplasmic reticulum. Requires manganese.

**References:** [2701, 2282]

[EC 3.5.3.9 created 1972, modified 2010]

**EC 3.5.3.10**

**Accepted name:** D-arginase

**Reaction:** D-arginine + H\(_2\)O = D-ornithine + urea

**Systematic name:** D-arginine amidinohydrolase

**References:** [1750]

[EC 3.5.3.10 created 1972]

**EC 3.5.3.11**

**Accepted name:** agmatinase

**Reaction:** agmatine + H\(_2\)O = putrescine + urea

**Other name(s):** agmatine ureohydrolase; SpeB

**Systematic name:** agmatine amidinohydrolase

**References:** [1015, 2693]

[EC 3.5.3.11 created 1972]

**EC 3.5.3.12**

**Accepted name:** agmatine deiminase

**Reaction:** agmatine + H\(_2\)O = \(N\)-carbamoylputrescine + NH\(_3\)

**Other name(s):** agmatine amidinohydrolase

**Systematic name:** agmatine iminohydrolase

**Comments:** The plant enzyme also catalyses the reactions of EC 2.1.3.3 (ornithine carbamoyltransferase), EC 2.1.3.6 (putrescine carbamoyltransferase) and EC 2.7.2.2 (carbamate kinase), thus functioning as a putrescine synthase, converting agmatine and ornithine into putrescine and citrulline, respectively.

**References:** [2370, 2410]

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EC 3.5.3.13
Accepted name: formimidoylglutamate deiminase
Reaction: \( N\text{-formimidoyl-L-glutamate} + H_2O = N\text{-formyl-L-glutamate} + NH_3 \)
Other name(s): formiminoglutamate deiminase; formiminoglutamic iminohydrolase
Systematic name: \( N\text{-formimidoyl-L-glutamate iminohydrolase} \)
References: [2792]

[EC 3.5.3.13 created 1975, modified 2000]

EC 3.5.3.14
Accepted name: amidinoaspartase
Reaction: \( N\text{-amidino-L-aspartate} + H_2O = L\text{-aspartate} + \text{urea} \)
Other name(s): amidinoaspartic amidinohydrolase
Systematic name: \( N\text{-amidino-L-aspartate amidinohydrolase} \)
Comments: Also acts slowly on \( N\text{-amidino-L-glutamate} \).
References: [1666]

[EC 3.5.3.14 created 1976]

EC 3.5.3.15
Accepted name: protein-arginine deiminase
Reaction: \( \text{protein-L-arginine} + H_2O = \text{protein-L-citrulline} + NH_3 \)
Other name(s): peptidylarginine deiminase
Systematic name: \( \text{protein-L-arginine iminohydrolase} \)
Comments: Also acts on \( N\text{-acyl-L-arginine} \) and, more slowly, on L-arginine esters.
References: [755]

[EC 3.5.3.15 created 1983]

EC 3.5.3.16
Accepted name: methylguanidinase
Reaction: \( \text{methylguanidine} + H_2O = \text{methylamine} + \text{urea} \)
Other name(s): methylguanidine hydrolase
Systematic name: \( \text{methylguanidine amidinohydrolase} \)
Comments: Acts on some other alkylguanidines, but very slowly.
References: [1769]

[EC 3.5.3.16 created 1984]

EC 3.5.3.17
Accepted name: guanidinopropionase
Reaction: \( 3\text{-guanidinopropanoate} + H_2O = \beta\text{-alanine} + \text{urea} \)
Other name(s): GPase; GPH
Systematic name: \( 3\text{-guanidinopropanoate amidinopropionase} \)
Comments: Requires Mn\(^{2+}\). Also acts, more slowly, on taurocynamine and 4-guanidinobutanoate.
References: [2890]

[EC 3.5.3.17 created 1989]

EC 3.5.3.18

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Accepted name: dimethylargininase
Reaction: $N^{\omega},N^{\omega'}$-dimethyl-L-arginine + H$_2$O = dimethylamine + L-citrulline
Other name(s): dimethylargininidimethylaminohydrolase; $N^{\omega},N^{\omega'}$-dimethylarginine dimethylaminohydrolase; $N^{\omega}$, $N^{\omega'}$-dimethyl-L-arginine dimethylamidohydrolase; $\omega,\omega'$-di-N-methyl-L-arginine dimethylaminohydrolase; $N^{\omega}$, $N^{\omega'}$-methyl-L-arginine dimethylamidohydrolase (incorrect)
Systematic name: $N^{\omega},N^{\omega'}$-dimethyl-L-arginine dimethylamidohydrolase
Comments: Also acts on $N^{\omega}$-methyl-L-arginine.
References: [1869]

[EC 3.5.3.18 created 1992]

EC 3.5.3.19
Accepted name: ureidoglycolate hydrolase
Reaction: $(S)$-ureidoglycolate + H$_2$O = glyoxylate + 2 NH$_3$ + CO$_2$
Systematic name: $(S)$-ureidoglycolate amidohydrolase (decarboxylating)
References: [2810]

[EC 3.5.3.19 created 1992]

EC 3.5.3.20
Accepted name: diguanidinobutanase
Reaction: 1,4-diguanidinobutane + H$_2$O = agmatine + urea
Systematic name: 1,4-diguanidinobutane amidinohydrolase
Comments: Other diguanidinoalkanes with 3 to 10 methylene groups can also act, but more slowly.
References: [2887]

[EC 3.5.3.20 created 1992]

EC 3.5.3.21
Accepted name: methylenediurea deaminase
Reaction: (1a) NH$_2$-CO-NH-CH$_2$-NH-CO-NH$_2$ + H$_2$O = $N$-(carboxyaminomethyl)urea + NH$_3$
(1b) $N$-(carboxyaminomethyl)urea = $N$-(aminomethyl)urea + CO$_2$ (spontaneous)
(1c) $N$-(aminomethyl)urea + H$_2$O = $N$-(hydroxymethyl)urea + NH$_3$ (spontaneous)
Other name(s): methylenediurease
Systematic name: methylenediurea aminohydrolase
Comments: The methylenediurea is hydrolysed and decarboxylated to give an aminated methylurea, which then spontaneously hydrolyses to hydroxymethylurea. The enzyme from *Ochrobactrum anthropi* also hydrolyses dimethylenetriurea and trimethylenetetraurea as well as ureidoglycolate, which is hydrolysed to urea and glyoxylate, and allantoate, which is hydrolysed to ureidoglycolate, ammonia and carbon dioxide.
References: [1123]

[EC 3.5.3.21 created 1999]

EC 3.5.3.22
Accepted name: proclavaminate amidinohydrolase
Reaction: amidinoproclavamate + H$_2$O = proclavamate + urea
Other name(s): PAH; proclavamate amidino hydrolase
Systematic name: amidinoproclavamate amidinohydrolase
Comments: Forms part of the pathway for the biosynthesis of the β-lactamase inhibitor clavulanate in *Streptomycetes clavuligerus*. It carries out an intermediary reaction between the first reaction of EC 1.14.11.21, clavaminate synthase, and the second and third reactions of that enzyme. Requires Mn$^{2+}$.
References: [2193, 2918, 2589, 2830]
EC 3.5.3.23

Accepted name: N-succinylarginine dihydrolase

Reaction: \( \text{N}^2\text{-succinyl-L-arginine} + 2 \text{H}_2\text{O} = \text{N}^2\text{-succinyl-L-ornithine} + 2 \text{NH}_3 + \text{CO}_2 \)

Other name(s): N\(^2\)succinylarginine dihydrolase; arginine succinylhydrolase; SADH; AruB; AstB; 2-N\(^2\)succinyl-L-arginine iminohydrolase (decarboxylating)

Systematic name: N\(^2\)succinyl-L-arginine iminohydrolase (decarboxylating)

Comments: Arginine, N\(^2\)acetylarginine and N\(^2\)-glutamylarginine do not act as substrates [2757]. This is the second enzyme in the arginine succinyltransferase (AST) pathway for the catabolism of arginine [2251]. 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 \( \text{N}^2 \)-succinyltransferase), EC 3.5.3.23 (\( \text{N}^2 \)-succinylarginine dihydrolase), EC 2.6.1.81 (succinylornithine transaminase), EC 1.2.1.71 (succinylglutamate semialdehyde dehydrogenase) and EC 3.5.1.96 (succinylglutamate desuccinylase).

References: [2251, 2568, 2757, 463, 1105]

EC 3.5.4 In cyclic amidines

EC 3.5.4.1

Accepted name: cytosine deaminase

Reaction: cytosine + H\(\text{2}\)_\(\text{O}\) = uracil + NH\(\text{3}\)

Other name(s): isocytosine deaminase

Systematic name: cytosine aminohydrolase

Comments: Also acts on 5-methylcytosine.

References: [418, 1327]

EC 3.5.4.2

Accepted name: adenine deaminase

Reaction: adenine + H\(\text{2}\)_\(\text{O}\) = hypoxanthine + NH\(\text{3}\)

Other name(s): adenase; adenine aminase; ADase

Systematic name: adenine aminohydrolase

References: [222, 991]

EC 3.5.4.3

Accepted name: guanine deaminase

Reaction: guanine + H\(\text{2}\)_\(\text{O}\) = xanthine + NH\(\text{3}\)

Other name(s): guanase; guanine aminase; GAH

Systematic name: guanine aminohydrolase

References: [1016, 1178, 2033]

EC 3.5.4.4

Accepted name: adenosine deaminase
Reaction: $\text{adenosine} + \text{H}_2\text{O} = \text{inosine} + \text{NH}_3$

Other name(s): deoxyadenosine deaminase

Systematic name: adenosine aminohydrolase

References: [1201, 2015]

EC 3.5.4.5
Accepted name: cytidine deaminase
Reaction: $\text{cytidine} + \text{H}_2\text{O} = \text{uridine} + \text{NH}_3$
Other name(s): cytosine nucleoside deaminase
Systematic name: cytidine aminohydrolase
References: [2121, 2738]

EC 3.5.4.6
Accepted name: AMP deaminase
Reaction: $\text{AMP} + \text{H}_2\text{O} = \text{IMP} + \text{NH}_3$
Other name(s): adenylc acid deaminase; AMP aminase; adenylc deaminase; adenylate deaminase; 5-AMP deaminase; adenosine 5-monophosphate deaminase; 5-adenylate deaminase; adenylic acid deaminase; adenosine monophosphate deaminase; adenylate aminohydrolase; adenylic desaminase; adenosine 5-phosphate aminohydrolase; 5-adenylate deaminase
Systematic name: AMP aminohydrolase
Comments: cf. EC 3.5.4.17 adenosine-phosphate deaminase.
References: [1178, 1409, 1410, 1411, 1636, 2628, 2770]

EC 3.5.4.7
Accepted name: ADP deaminase
Reaction: $\text{ADP} + \text{H}_2\text{O} = \text{IDP} + \text{NH}_3$
Other name(s): adenosine diphosphate deaminase; adenosinepyrophosphate deaminase
Systematic name: ADP aminohydrolase
References: [530]

EC 3.5.4.8
Accepted name: aminomimidazolase
Reaction: $\text{4-aminomimidazole} + \text{H}_2\text{O} = \text{imidazol-4-one} + \text{NH}_3$
Other name(s): 4-aminomimidazole hydrolase; 4-aminomimidazole deaminase
Systematic name: 4-aminomimidazole aminohydrolase
Comments: Requires Fe$^{2+}$. This enzyme forms part of the xanthine-degradation pathway in some bacteria. The product of the reaction, imidazol-4-one, can be converted non-enzymically into formiminoglycine. An enzyme has been identified in Clostridium cylindrosporum that can perform this hydrolysis reaction.
References: [726, 2702]

EC 3.5.4.9
Accepted name: methenyltetrahydrofolate cyclohydrolase
Reaction: 5,10-methenyltetrahydrofolate + H₂O = 10-formyltetrahydrofolate
Other name(s): Citrovorum factor cyclodehydrase; cyclohydrolase; formyl-methenyl-methylene-tetrahydrofolate synthetase (combined)
Systematic name: 5,10-methenyltetrahydrofolate 5-hydrolase (decyclizing)
Comments: In eukaryotes, the enzyme occurs as a trifunctional enzyme that also has methylenetetrahydrofolate dehydrogenase (NADP⁺) (EC 1.5.1.5) and formate—tetrahydrofolate ligase (EC 6.3.4.3) activity. In some prokaryotes, it occurs as a bifunctional enzyme that also has dehydrogenase (EC 1.5.1.5) activity or formimidoyltetrahydrofolate cyclodeaminase (EC 4.3.1.4) activity.
References: [2035, 2474]

[EC 3.5.4.9 created 1961]

EC 3.5.4.10
Accepted name: IMP cyclohydrolase
Reaction: IMP + H₂O = 5-formamido-1-(5-phospho-D-ribosyl)imidazole-4-carboxamide
Other name(s): inosinicase; inosinate cyclohydrolase
Systematic name: IMP 1,2-hydrolase (decyclizing)
References: [698]

[EC 3.5.4.10 created 1961, modified 2000]

EC 3.5.4.11
Accepted name: pterin deaminase
Reaction: 2-amino-4-hydroxypteridine + H₂O = 2,4-dihydroxypteridine + NH₃
Other name(s): acrasinase
Systematic name: 2-amino-4-hydroxypteridine aminohydrolase
Comments: The animal enzyme is specific for pterin, isoxanthopterin and tetrahydropterin.
References: [1427, 2093]

[EC 3.5.4.11 created 1965]

EC 3.5.4.12
Accepted name: dCMP deaminase
Reaction: dCMP + H₂O = dUMP + NH₃
Other name(s): deoxycytidylate deaminase; deoxy-CMP-deaminase; deoxycytidylate aminohydrolase; deoxycytidine monophosphate deaminase; deoxycytidine-5'-phosphate deaminase; deoxycytidine-5'-monophosphate aminohydrolase
Systematic name: dCMP aminohydrolase
Comments: Also acts on some 5-substituted dCMPs.
References: [2226, 2227, 2279]

[EC 3.5.4.12 created 1965]

EC 3.5.4.13
Accepted name: dCTP deaminase
Reaction: dCTP + H₂O = dUTP + NH₃
Other name(s): deoxycytidine triphosphate deaminase; 5-methyl-dCTP deaminase
Systematic name: dCTP aminohydrolase
References: [2573]

[EC 3.5.4.13 created 1972]
EC 3.5.4.14

Accepted name: deoxycytidine deaminase
Reaction: deoxycytidine + H₂O = deoxyuridine + NH₃
Systematic name: deoxycytidine aminohydrolase
References: [417]

[EC 3.5.4.14 created 1972]

EC 3.5.4.15

Accepted name: guanosine deaminase
Reaction: guanosine + H₂O = xanthosine + NH₃
Other name(s): guanosine aminase
Systematic name: guanosine aminohydrolase
References: [1101]

[EC 3.5.4.15 created 1972]

EC 3.5.4.16

Accepted name: GTP cyclohydrolase I
Reaction: GTP + H₂O = formate + 7,8-dihydroneopterin 3′-triphosphate
Other name(s): GTP cyclohydrolase; guanosine triphosphate cyclohydrolase; guanosine triphosphate 8-deformylase; dihydroneopterin triphosphate synthase; GTP 8-formylhydrolase
Systematic name: GTP 7,8-8,9-dihydrolase
Comments: The reaction involves hydrolysis of two C-N bonds and isomerization of the pentose unit; the recyc- lization may be non-enzymic. This enzyme is involved in the de novo synthesis of tetrahydrobiopterin from GTP, with the other enzymes involved being EC 1.1.1.153 (sepiapterin reductase) and EC 4.2.3.12 (6-pyruvoyltetrahydropterin synthase) [2454].
References: [302, 2820, 2454]

[EC 3.5.4.16 created 1972]

EC 3.5.4.17

Accepted name: adenosine-phosphate deaminase
Reaction: 5′-AMP + H₂O = 5′-IMP + NH₃
Other name(s): adenylate deaminase; adenine nucleotide deaminase; adenosine (phosphate) deaminase
Systematic name: adenosine-phosphate aminohydrolase
Comments: Acts on 5′-AMP, ADP, ATP, NAD⁺ and adenosine, in decreasing order of activity. The bacterial en- zyme also acts on the deoxy derivatives. cf. EC 3.5.4.6 AMP deaminase.
References: [2437, 2875]

[EC 3.5.4.17 created 1972, modified 1980]

EC 3.5.4.18

Accepted name: ATP deaminase
Reaction: ATP + H₂O = ITP + NH₃
Other name(s): adenosine triphosphate deaminase
Systematic name: ATP aminohydrolase
References: [405]

[EC 3.5.4.18 created 1972]

EC 3.5.4.19

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Accepted name: phosphoribosyl-AMP cyclohydrolase
Reaction: \(1-(5\text{-phosphoribosyl})\text{-AMP} + \text{H}_2\text{O} = 1-(5\text{-phosphoribosyl})\text{-5-[(5-phosphoribosylamino)methylideneamino]imidazole-4-carboxamide}\)
Other name(s): PRAMP-cyclohydrolase; phosphoribosyladenosine monophosphate cyclohydrolase
Systematic name: 1-(5-phospho-\(D\)-ribosyl)-AMP 1,6-hydrolase
Comments: The *Neurospora crassa* enzyme also catalyses the reactions of EC 1.1.1.23 (histidinol dehydrogenase) and EC 3.6.1.31 (phosphoribosyl-ATP diphosphatase).
References: [1671]

EC 3.5.4.20
Accepted name: pyrithiamine deaminase
Reaction: \(1-(4\text{-amino-2-methylpyrimid-5-ylmethyl})\text{-3-(\(\beta\)-hydroxyethyl)-2-methylpyridinium bromide} + \text{H}_2\text{O} = 1-(4\text{-hydroxy-2-methylpyrimid-5-ylmethyl})\text{-3-(\(\beta\)-hydroxyethyl)-2-methylpyridinium bromide} + \text{NH}_3\)
Systematic name: 1-(4-amino-2-methylpyrimid-5-ylmethyl)-3-(\(\beta\)-hydroxyethyl)-2-methylpyridinium-bromide aminohydrolase
References: [2340]

EC 3.5.4.21
Accepted name: creatinine deaminase
Reaction: creatinine + \(\text{H}_2\text{O} = N\text{-methylhydantoin} + \text{NH}_3\)
Other name(s): creatinine hydrolase; creatinine desiminase
Systematic name: creatinine iminohydrolase
References: [2470]

EC 3.5.4.22
Accepted name: 1-pyrroline-4-hydroxy-2-carboxylate deaminase
Reaction: 1-pyrroline-4-hydroxy-2-carboxylate + \(\text{H}_2\text{O} = 2,5\text{-dioxopentanoate} + \text{NH}_3\)
Other name(s): HPC deaminase
Systematic name: 1-pyrroline-4-hydroxy-2-carboxylate aminohydrolase (decyclizing)
References: [2338, 2339]

EC 3.5.4.23
Accepted name: blasticidin-S deaminase
Reaction: blasticidin S + \(\text{H}_2\text{O} = \text{deaminohydroxyblasticidin S} + \text{NH}_3\)
Systematic name: blasticidin-S aminohydrolase
Comments: Catalyses the deamination of the cytosine moiety of the antibiotics blasticidin S, cytomyein and acetylblasticidin S.
References: [2845]

EC 3.5.4.24
Accepted name: sepiapterin deaminase
Reaction: sepiapterin + \(\text{H}_2\text{O} = \text{xanthopterin-B2} + \text{NH}_3\)
**Systematic name:** sepiapterin aminohydrolase
**Comments:** Also acts on isosepiapterin, but more slowly.
**References:** [2620]

[EC 3.5.4.24 created 1976]

**EC 3.5.4.25**
**Accepted name:** GTP cyclohydrolase II
**Reaction:** GTP + 3 $\text{H}_2\text{O}$ = formate + 2,5-diamino-6-hydroxy-4-(5-phosphoribosylamino)pyrimidine + diphosphate
**Other name(s):** guanosine triphosphate cyclohydrolase II; GTP-8-formylhydrolase
**Systematic name:** GTP 7,8-8,9-dihydrolase (diphosphate-forming)
**Comments:** Two C-N bonds are hydrolysed, releasing formate, with simultaneous removal of the terminal diphosphate.
**References:** [714]

[EC 3.5.4.25 created 1984]

**EC 3.5.4.26**
**Accepted name:** diaminoxyphosphoribosylaminopyrimidine deaminase
**Reaction:** 2,5-diamino-6-hydroxy-4-(5-phosphoribosylamino)pyrimidine + $\text{H}_2\text{O}$ = 5-amino-6-(5-phosphoribosylamino)uracil + NH$_3$
**Systematic name:** 2,5-diamino-6-hydroxy-4-(5-phosphoribosylamino)pyrimidine 2-aminohydrolase
**Comments:** The substrate is the product of EC 3.5.4.25 GTP cyclohydrolase II.
**References:** [304]

[EC 3.5.4.26 created 1984]

**EC 3.5.4.27**
**Accepted name:** methenyltetrahydromethanopterin cyclohydrolase
**Reaction:** 5,10-methenyl-5,6,7,8-tetrahydromethanopterin + $\text{H}_2\text{O}$ = 5-formyl-5,6,7,8-tetrahydromethanopterin
**Other name(s):** 5,10-methenyltetrahydromethanopterin cyclohydrolase; $N^5,N^{10}$-methenyltetrahydromethanopterin cyclohydrolase; methenyl-H$_4$MPT cyclohydrolase
**Systematic name:** 5,10-methenyltetrahydromethanopterin 10-hydrolase (decyclizing)
**Comments:** Methanopterin is a pterin analogue. The enzyme is involved in the formation of methane from CO$_2$ in *Methanobacterium thermoautotrophicum*.
**References:** [570]

[EC 3.5.4.27 created 1989]

**EC 3.5.4.28**
**Accepted name:** S-adenosylhomocysteine deaminase
**Reaction:** S-adenosyl-L-homocysteine + $\text{H}_2\text{O}$ = S-inosyl-L-homocysteine + NH$_3$
**Other name(s):** adenosylhomocysteine deaminase
**Systematic name:** S-adenosyl-L-homocysteine aminohydrolase
**References:** [2930]

[EC 3.5.4.28 created 1992]

**EC 3.5.4.29**
**Accepted name:** GTP cyclohydrolase IIa
**Reaction:** GTP + 3 $\text{H}_2\text{O}$ = 2-amino-5-formylamino-6-(5-phosphoribosylamino)pyrimidin-4(3H)-one + 2 phosphate

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**Systematic name:** GTP 8,9-hydrolase (phosphate-forming)

**Comments:** Requires Mg$^{2+}$. This enzyme catalyses the hydrolysis of the imidazole ring of guanosine 5′-triphosphate, N$^7$-methylguanosine 5′-triphosphate or inosine 5′-triphosphate. Xanthosine 5′-triphosphate and ATP are not substrates. It also catalyses the hydrolysis of diphosphate to form two equivalents of phosphate. Unlike GTP cyclohydrolase II (EC 3.5.4.25), this enzyme does not release formate, but does hydrolyse the diphosphate from GTP to phosphate.

**References:** [855]

**EC 3.5.4.30**

**Accepted name:** dCTP deaminase (dUMP-forming)

**Reaction:** dCTP + 2 H$_2$O = dUMP + diphosphate + NH$_3$

**Systematic name:** dCTP aminohydrolase (dUMP-forming)

**Comments:** Requires Mg$^{2+}$. Is highly specific for dCTP as substrate as dCMP, CTP, CDP, CMP, cytosine or deoxyctosine are not deaminated. While most bacteria require two enzymes to form dUMP from dCTP (EC 3.5.4.13, dCTP deaminase and EC 3.6.1.23, dUTP diphosphatase), the archaeon *Methanocaldococcus jannaschii* uses a single enzyme to carry out both functions. This enzyme can also act as a dUTP diphosphatase, but more slowly.

**References:** [1438]

**EC 3.5.5 In nitriles**

**EC 3.5.5.1**

**Accepted name:** nitrilase

**Reaction:** a nitrile + 2 H$_2$O = a carboxylate + NH$_3$

**Other name(s):** acetonitrilase; benzonitrilase

**Systematic name:** nitrile aminohydrolase

**Comments:** Acts on a wide range of aromatic nitriles including (indol-3-yl)acetonitrile, and also on some aliphatic nitriles, and on the corresponding acid amides. *cf.* EC 4.2.1.84 nitrile hydratase.

**References:** [932, 2548, 1925]

[EC 3.5.5.1 created 1965, modified 1989]

**EC 3.5.5.2**

**Accepted name:** ricinine nitrilase

**Reaction:** ricinine + 2 H$_2$O = 3-carboxy-4-methoxy-N-methyl-2-pyridone + NH$_3$

**Systematic name:** ricinine aminohydrolase

**References:** [2129, 1035, 1925]

[EC 3.5.5.2 created 1972]

[3.5.5.3 *Transferred entry. cyanate hydratase. Now EC 4.2.1.104, cyanate hydratase*]

[EC 3.5.5.3 created 1972, deleted 1990]

**EC 3.5.5.4**

**Accepted name:** cyanoalanine nitrilase

**Reaction:** 3-cyano-L-alanine + 2 H$_2$O = L-aspartate + NH$_3$

**Other name(s):** β-cyanoalanine nitrilase

**Systematic name:** 3-cyano-L-alanine aminohydrolase

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L-Asparagine is formed as an intermediate.

References: [2855]

[EC 3.5.5.4 created 1986]

**EC 3.5.5.5**

Accepted name: arylacetonitrilase

Reaction: 4-chlorophenylacetonitrile + 2 H₂O = 4-chlorophenylacetate + NH₃

Systematic name: arylacetonitrile aminohydrolase

Comments: Requires thiol compounds. Also hydrolyses other 4-substituted phenylacetonitriles, thien-2-ylacetonitrile, tolylacetonitriles, and, more slowly, benzyl cyanide.

References: [1601, 1753]

[EC 3.5.5.5 created 1992]

**EC 3.5.5.6**

Accepted name: bromoxynil nitrilase

Reaction: 3,5-dibromo-4-hydroxybenzonitrile + 2 H₂O = 3,5-dibromo-4-hydroxy-benzoate + NH₃

Systematic name: 3,5-dibromo-4-hydroxybenzonitrile aminohydrolase

Comments: Involved in the bacterial degradation of the herbicide bromoxynil. Highly specific.

References: [2413]

[EC 3.5.5.6 created 1992]

**EC 3.5.5.7**

Accepted name: aliphatic nitrilase

Reaction: R-CN + 2 H₂O = R-COOH + NH₃

Systematic name: aliphatic nitrile aminohydrolase

Comments: Preferentially hydrolyses aliphatic nitriles, some of which are apparently not substrates for other known nitrilases (EC 3.5.5.1). Substrates include crotononitrile, acrylonitrile and glutaronitrile.

References: [1293, 1925]

[EC 3.5.5.7 created 1999]

**EC 3.5.5.8**

Accepted name: thiocyanate hydrolase

Reaction: thiocyanate + 2 H₂O = carbonyl sulfide + NH₃ + HO⁻

Systematic name: thiocyanate aminohydrolase

Comments: The enzyme from *Thiobacillus thioparus* catalyses the first step in the degradation of thiocyanate.

References: [1208, 1209]

[EC 3.5.5.8 created 2000]

**EC 3.5.99 In other compounds**

**EC 3.5.99.1**

Accepted name: riboflavinase

Reaction: riboflavin + H₂O = ribitol + lumichrome

Systematic name: riboflavin hydrolase

References: [2854]
EC 3.5.99.1

Accepted name: thiaminase
Reaction: thiamine + H₂O = 4-amino-5-hydroxymethyl-2-methylpyrimidine + 5-(2-hydroxyethyl)-4-methylthiazole
Other name(s): thiaminase II
Systematic name: thiamine hydrolase
References: [757, 1077]

EC 3.5.99.2

Accepted name: hydroxydechloroatrazine ethylaminohydrolase
Reaction: 4-(ethylamino)-2-hydroxy-6-(isopropylamino)-1,3,5-triazine + H₂O = N-isopropylammelide + ethylamine
Other name(s): AtzB; hydroxyatrazine ethylaminohydrolase
Systematic name: 4-(ethylamino)-2-hydroxy-6-(isopropylamino)-1,3,5-triazine ethylaminohydrolase
Comments: Involved in a pathway by which the herbicide atrazine, 2-chloro-4-(ethylamino)-6-(isopropylamino)-1,3,5-triazine, is degraded in bacteria via N-isopropylammelide, 2,4-dihydroxy-6-(isopropylamino)-1,3,5-triazine.
References: [246]

EC 3.5.99.3

Accepted name: N-isopropylammelide isopropylaminohydrolase
Reaction: N-isopropylammelide + H₂O = cyanuric acid + isopropylamine
Other name(s): AtzC
Systematic name: N-isopropylammelide isopropylaminohydrolase
Comments: Involved in a pathway by which the herbicide atrazine, 2-chloro-4-(ethylamino)-6-(isopropylamino)-1,3,5-triazine, is degraded in bacteria via N-isopropylammelide, 2,4-dihydroxy-6-(isopropylamino)-1,3,5-triazine.
References: [2176]

EC 3.5.99.4

Accepted name: 2-aminomuconate deaminase
Reaction: 2-aminomuconate + H₂O = 4-oxaloacetoate + NH₃
Systematic name: 2-aminomuconate aminohydrolase
Comments: Intermediate in the biodegradation of nitrobenzene by Pseudomonas pseudocaligenes JS45. The reaction is spontaneous in acid conditions.
References: [966, 965]

EC 3.5.99.5

Accepted name: glucosamine-6-phosphate deaminase
Reaction: D-glucosamine 6-phosphate + H₂O = D-fructose 6-phosphate + NH₃
Other name(s): glucosaminephosphate isomerase; glucosamine-6-phosphate isomerase; phosphoglucominiso- merase; glucosamine phosphate deaminase; aminodeoxyglucosephosphate isomerase; phosphoglu- cosamine isomerase

Reference: 259
Systematic name: 2-amino-2-deoxy-D-glucose-6-phosphate aminohydrolase (ketol isomerizing)
Comments: Isomerization of the aldose-ketose type converts the -CH(-NH$_2$)-CH=O group of glucosamine 6-phosphate into -C(=NH)-CH$_2$-OH, forming 2-deoxy-2-imino-D-arabino-hexitol, which then hydrolizes to yield fructose 6-phosphate and ammonia. N-Acetyl-D-glucosamine 6-phosphate, which is not broken down, activates the enzyme.
References: [422, 1946, 2821]

[EC 3.5.99.6 created 1961 as EC 5.3.1.10, transferred 2000 to EC 3.5.99.6]

EC 3.5.99.7
Accepted name: 1-aminocyclopropane-1-carboxylate deaminase
Reaction: 1-aminocyclopropane-1-carboxylate + H$_2$O = 2-oxobutanoate + NH$_3$
Other name(s): 1-aminocyclopropane-1-carboxylate endolyase (deaminating)
Systematic name: 1-aminocyclopropane-1-carboxylate aminohydrolase (isomerizing)
Comments: A pyridoxal 5'-phosphate enzyme. Its introduction has been used to make fruit ripening dependent on externally added ethylene, as it removes the substrate for endogenous ethylene formation.
References: [1033, 2860]

[EC 3.5.99.7 created 1981 as EC 4.1.99.4, transferred 2002 to EC 3.5.99.7]

EC 3.6 Acting on acid anhydrides

To this subclass belong mainly the enzymes acting on diphosphate bonds in compounds such as nucleoside di- and tri-phosphates (EC 3.6.1), on sulfonyl-containing anhydrides such as adenylylsulfate (EC 3.6.2) and on acid anhydrides; catalysing transmembrane movement of substances (EC 3.6.3).

EC 3.6.1 In phosphorus-containing anhydrides

EC 3.6.1.1
Accepted name: inorganic diphosphatase
Reaction: diphosphate + H$_2$O = 2 phosphate
Systematic name: diphosphate phosphohydrolase
Comments: Specificity varies with the source and with the activating metal ion. The enzyme from some sources may be identical with EC 3.1.3.1 (alkaline phosphatase) or EC 3.1.3.9 (glucose-6-phosphatase). A form of this enzyme with a molecular mass of about 90 kDa is found in tonoplasts of plants and fungi, where it imports protons from the cytosol into the vacuolar lumen.
References: [106, 1348, 2041]

[EC 3.6.1.1 created 1961, modified 2000]

EC 3.6.1.2
Accepted name: trimetaphosphatase
Reaction: trimetaphosphate + H$_2$O = triphosphate
Other name(s): inorganic trimetaphosphatase
Systematic name: trimetaphosphate hydrolase
References: [1311, 1647]

[EC 3.6.1.2 created 1961]

EC 3.6.1.3
Accepted name: adenosinetriphosphatase

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**Reaction:** ATP + H₂O = ADP + phosphate

**Other name(s):** adenylypyrophosphatase; ATP monophosphatase; triphosphatase; ATPase; SV40 T-antigen; adenosine 5'-triphosphatase; ATP hydrolase; ATPase; complex V (mitochondrial electron transport); (Ca²⁺ + Mg²⁺)-ATPase; HCO₃⁻-ATPase; adenosine triphosphatase

**Systematic name:** ATP phosphohydrolase

**Comments:** Many enzymes previously listed under this number are now listed separately under EC 3.6.3 and EC 3.6.4.

**References:** [793, 1248, 1575, 1821, 2113, 2566]

[EC 3.6.1.3 created 1961 (EC 3.6.1.4 created 1961, incorporated 1965)]

**3.6.1.4** Deleted entry. adenosinetriphosphatase (Mg-activated). Now included with EC 3.6.1.3 adenosinetriphosphatase

[EC 3.6.1.4 created 1961, deleted 1965]

**EC 3.6.1.5**

**Accepted name:** apyrase

**Reaction:** ATP + 2 H₂O = AMP + 2 phosphate

**Other name(s):** ATP-diphosphatase; adenosine diphosphatase; ADPase; ATP diphosphohydrolase [ambiguous]

**Systematic name:** ATP diphosphohydrolase (phosphate-forming)

**Comments:** Requires Ca²⁺. Also acts on ADP, and on other nucleoside triphosphates and diphosphates. Most of the ecto-ATPases occurring on the cell surface and hydrolysing extracellular nucleoside triphosphates and diphosphates belong to this enzyme family. Either Ca²⁺ or Mg²⁺ can serve as activating ions.

**References:** [1331, 1453]

[EC 3.6.1.5 created 1961, modified 1976, modified 2000]

**EC 3.6.1.6**

**Accepted name:** nucleoside-diphosphatase

**Reaction:** a nucleoside diphosphate + H₂O = a nucleotide + phosphate

**Other name(s):** thiaminpyrophosphatase; UDPase; inosine diphosphatase; adenosine diphosphatase; IDPase; ADPase; adenosinepyrophosphatase; guanosine diphosphatase; guanosine 5'-diphosphatase; inosine 5'-diphosphatase; uridine diphosphatase; uridine 5'-diphosphatase; nucleoside diphosphate phosphatase; type B nucleoside diphosphatase; GDPase; CDPase; nucleoside 5'-diphosphatase; type L nucleoside diphosphatase; NDPase; nucleoside diphosphate phosphohydrolase

**Systematic name:** nucleoside-diphosphate phosphohydrolase

**Comments:** Acts on IDP, GDP, UDP and also on D-ribose 5-diphosphate

**References:** [810, 1039]

[EC 3.6.1.6 created 1961]

**EC 3.6.1.7**

**Accepted name:** acylphosphatase

**Reaction:** an acylphosphate + H₂O = a carboxylate + phosphate

**Other name(s):** acetylphosphatase; 1,3-diphosphoglycerate phosphatase; acetic phosphatase; Ho 1-3; GP 1-3

**Systematic name:** acylphosphate phosphohydrolase

**References:** [2044, 2052, 2053, 2310]

[EC 3.6.1.7 created 1961]

**EC 3.6.1.8**

**Accepted name:** ATP diphosphatase

**Reaction:** ATP + H₂O = AMP + diphosphate

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Other name(s): ATPase; ATP pyrophosphatase; adenosine triphosphate pyrophosphatase; ATP diphosphohydrolase
Systematic name: ATP diphosphohydrolase (diphosphate-forming)
Comments: Also acts on ITP, GTP, CTP and UTP.
References: [990, 1150]

[EC 3.6.1.8 created 1961]

EC 3.6.1.9
Accepted name: nucleotide diphosphatase
Reaction: a dinucleotide + H₂O = 2 mononucleotides
Other name(s): nucleotide pyrophosphatase; nucleotide-sugar pyrophosphatase
Systematic name: dinucleotide nucleotidohydrolase
Comments: Substrates include NAD⁺, NADP⁺, FAD, CoA and also ATP and ADP.
References: [1117, 1310, 1343, 2468]

[EC 3.6.1.9 created 1961]

EC 3.6.1.10
Accepted name: endopolyphosphatase
Reaction: polyphosphate + n H₂O = (n+1) oligophosphate
Other name(s): polyphosphate depolymerase; metaphosphatase; polyphosphatase; polymetaphosphatase
Systematic name: polyphosphate polyphosphohydrolase
Comments: The product contains 4 or 5 phosphate residues.
References: [1550, 1597]

[EC 3.6.1.10 created 1961]

EC 3.6.1.11
Accepted name: exopolyphosphatase
Reaction: (polyphosphate)ₙ + H₂O = (polyphosphate)ₙ₋₁ + phosphate
Other name(s): metaphosphatase; acid phosphoanhydride phosphohydrolase; Gra-Pase
Systematic name: polyphosphate phosphohydrolase
References: [881, 1331, 1550]

[EC 3.6.1.11 created 1965]

EC 3.6.1.12
Accepted name: dCTP diphosphatase
Reaction: dCTP + H₂O = dCMP + diphosphate
Other name(s): deoxycytidine-triphosphatase; dCTPase; dCTP pyrophosphatase; deoxyctydine triphosphatase;
deox-CTPase; dCTPase
Systematic name: dCTP nucleotidohydrolase
Comments: Also hydrolyses dCDP to dCMP and phosphate.
References: [2922]

[EC 3.6.1.12 created 1965]

EC 3.6.1.13
Accepted name: ADP-ribose diphosphatase
Reaction: ADP-ribose + H₂O = AMP + D-ribose 5-phosphate
Other name(s): ADP-ribosyl pyrophosphatase; adenosine diphosphoribose pyrophosphatase; ADPR-PPase

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<table>
<thead>
<tr>
<th><strong>Systematic name:</strong></th>
<th>ADP-ribose ribophosphohydrolase</th>
</tr>
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<tbody>
<tr>
<td><strong>References:</strong></td>
<td>[561]</td>
</tr>
</tbody>
</table>

[EC 3.6.1.13 created 1965]

### EC 3.6.1.14

**Accepted name:** adenosine-tetraphosphatase  
**Reaction:** adenosine 5′-tetraphosphate + H₂O = ATP + phosphate  
**Systematic name:** adenosine-tetraphosphate phosphohydrolase  
**Comments:** Also acts on inosine tetraphosphate and tripolyphosphate but shows little or no activity with other nucleotides or polyphosphates.  
**References:** [2362]

[EC 3.6.1.14 created 1972]

### EC 3.6.1.15

**Accepted name:** nucleoside-triphosphatase  
**Reaction:** NTP + H₂O = NDP + phosphate  
**Other name(s):** nucleoside triphosphate phosphohydrolase; nucleoside-5-triphosphate phosphohydrolase; nucleoside 5-triphosphatase  
**Systematic name:** unspecific diphosphate phosphohydrolase  
**Comments:** Also hydrolyses other nucleoside triphosphates, diphosphates, thiamine diphosphate and FAD.  
**References:** [269, 1434, 1593]

[EC 3.6.1.15 created 1972]

### EC 3.6.1.16

**Accepted name:** CDP-glycerol diphosphatase  
**Reaction:** CDP-glycerol + H₂O = CMP + sn-glycerol 3-phosphate  
**Other name(s):** CDP-glycerol pyrophosphatase; cytidine diphosphoglycerol pyrophosphatase  
**Systematic name:** CDP-glycerol phosphoglycerohydrolase  
**References:** [822]

[EC 3.6.1.16 created 1972]

### EC 3.6.1.17

**Accepted name:** bis(5′-nucleosyl)-tetraphosphatase (asymmetrical)  
**Reaction:** P¹,P¹-bis(5′-guanosyl) tetraphosphate + H₂O = GTP + GMP  
**Other name(s):** bis(5′-guanosyl)-tetraphosphatase; bis(5′-adenosyl)-tetraphosphatase; diguanosinetetraphosphatase (asymmetrical); dinucleosidetetraphosphatase (asymmetrical); diadenosine P¹,P³-tetraphosphatase; dinucleoside tetraphosphatase; 1-P,4-P-bis(5′-nucleosyl)-tetraphosphate nucleotidohydrolase  
**Systematic name:** P¹,P¹-bis(5′-nucleosyl)-tetraphosphate nucleotidohydrolase  
**Comments:** Also acts on bis(5′-xanthosyl)-tetraphosphate and, more slowly, on bis(5′-adenosyl)-tetraphosphate and bis(5′-uridylyl)-tetraphosphate [cf. EC 3.6.1.41 bis(5′-nucleosyl)-tetraphosphatase (symmetrical)]  
**References:** [1128, 2660, 2746]

[EC 3.6.1.17 created 1972, modified 1976, modified 1986]

### EC 3.6.1.18

**Accepted name:** FAD diphosphatase  
**Reaction:** FAD + H₂O = AMP + FMN

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Other name(s): FAD pyrophosphatase; riboflavin adenine dinucleotide pyrophosphatase; flavin adenine dinucleotide pyrophosphatase; riboflavin adenine dinucleotide pyrophosphatase; flavine adenine dinucleotide pyrophosphatase

Systematic name: FAD nucleotidohydrolase

Comments: The plant enzyme also hydrolyses NAD\(^+\) and NADH; the animal enzyme hydrolyses NAD\(^+\) and CoA at about half of the rate of hydrolysis of FAD. May be identical with EC 3.6.1.9 nucleotide diphosphatase.

References: [2066, 2306]

EC 3.6.1.19

Accepted name: nucleoside-triphosphate diphosphatase

Reaction: a nucleoside triphosphate + H\(_2\)O = a nucleotide + diphosphate

Other name(s): nucleoside-triphosphate pyrophosphatase

Systematic name: nucleoside-triphosphate diphosphohydrolase

Comments: May be identical with EC 3.6.1.9 nucleotide diphosphatase.

References: [385]

EC 3.6.1.20

Accepted name: 5′-acylphosphoadenosine hydrolase

Reaction: 5′-acylphosphoadenosine + H\(_2\)O = AMP + a carboxylate

Other name(s): 5-phosphoadenosine hydrolase

Systematic name: 5′-acylphosphoadenosine acylhydrolase

Comments: Also acts on inosine and uridine compounds.

References: [1225]

EC 3.6.1.21

Accepted name: ADP-sugar diphosphatase

Reaction: ADP-sugar + H\(_2\)O = AMP + \(\alpha\)-D-aldose 1-phosphate

Other name(s): ADP-sugar pyrophosphatase; adenosine diphosphosugar pyrophosphatase

Systematic name: ADP-sugar sugarphosphohydrolase

Comments: Has a specificity that is distinct from that of UDP-sugar diphosphatase (EC 3.6.1.45).

References: [2137]

EC 3.6.1.22

Accepted name: NAD\(^+\) diphosphatase

Reaction: NAD\(^+\) + H\(_2\)O = AMP + NMN

Other name(s): nicotinamide adenine dinucleotide pyrophosphatase; NADP pyrophosphatase; NADH pyrophosphatase

Systematic name: NAD\(^+\) phosphohydrolase

Comments: Also acts on NADP\(^+\), 3-acetylpyridine and the thionicotinamide analogues of NAD\(^+\) and NADP\(^+\).

References: [48, 1772]
EC 3.6.1.23

Accepted name: dUTP diphosphatase
Reaction: dUTP + H₂O = dUMP + diphosphate
Other name(s): deoxyuridine-triphosphatase; dUTPase; dUTP pyrophosphatase; deoxyuridine 5′-triphosphate nucleotidohydrolase; deoxyuridine 5′-triphosphatase
Systematic name: dUTP nucleotidohydrolase
References: [182, 821, 866, 870]

[EC 3.6.1.23 created 1972]

EC 3.6.1.24

Accepted name: nucleoside phosphoacylhydrolase
Reaction: Hydrolyses mixed phospho-anhydride bonds
Systematic name: nucleoside-5′-phosphoacylate acylhydrolase
Comments: Attacks ribonucleoside 5′-nitrophenylphosphates, but is inactive against phosphodiesters.
References: [2398]

[EC 3.6.1.24 created 1972]

EC 3.6.1.25

Accepted name: triphosphatase
Reaction: triphosphate + H₂O = diphosphate + phosphate
Other name(s): inorganic triphosphatase
Systematic name: triphosphate phosphohydrolase
References: [1339, 2641]

[EC 3.6.1.25 created 1976]

EC 3.6.1.26

Accepted name: CDP-diacylglycerol diphosphatase
Reaction: CDP-diacylglycerol + H₂O = CMP + phosphatidate
Other name(s): cytidine diphosphodiacylglycerol pyrophosphatase; CDP diacylglycerol hydrolase
Systematic name: CDP-diacylglycerol phosphatidylhydrolase
References: [2040]

[EC 3.6.1.26 created 1976]

EC 3.6.1.27

Accepted name: undecaprenyl-diphosphatase
Reaction: undecaprenyl diphosphate + H₂O = undecaprenyl phosphate + phosphate
Other name(s): C₅₅-isoprenyl diphosphatase; C₅₅-isoprenyl pyrophosphatase; isoprenyl pyrophosphatase
Systematic name: undecaprenyl-diphosphate phosphohydrolase
Comments: The undecaprenol involved is *ditrans,octacis*-undecaprenol (for definitions, click here).
References: [844]

[EC 3.6.1.27 created 1978, modified 2002]

EC 3.6.1.28

Accepted name: thiamine-triphosphatase
Reaction: thiamine triphosphate + H₂O = thiamine diphosphate + phosphate
Systematic name: thiamine-triphosphate phosphohydrolase
References: [944]

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EC 3.6.1.29

Accepted name: bis(5′-adenosyl)-triposphatase

Reaction: $P_1^1,P_3^3$-bis(5′-adenosyl) triphosphate + H$_2$O = ADP + AMP

Other name(s): dinucleosidetriphosphatase; diadenosine 5,5′-P$_1^1$,P$_3^3$-triphosphatase; 1-P,3-P-bis(5′-adenosyl)-triphosphate adenylylhydrolase

Systematic name: $P_1^1,P_3^3$-bis(5′-adenosyl)-triphosphate adenylylhydrolase

References: [1128, 2326]

EC 3.6.1.30

Accepted name: m$7^G$(5′)pppN diphosphatase

Reaction: 7-methylguanosine 5′-triphospho-5′-polynucleotide + H$_2$O = 7-methylguanosine 5′-phosphate + polynucleotide

Other name(s): decapase; m$7^G$(5′)pppN pyrophosphatase

Systematic name: 7-methylguanosine-5′-triphospho-5′-polynucleotide 7-methylguanosine-5′-phosphohydrolase

References: [1387, 1841, 1842]

EC 3.6.1.31

Accepted name: phosphoribosyl-ATP diphosphatase

Reaction: 1-(5-phosphoribosyl)-ATP + H$_2$O = 1-(5-phosphoribosyl)-AMP + diphosphate

Other name(s): phosphoribosyl-ATP pyrophosphatase; phosphoribosyladenosine triphosphate pyrophosphatase

Systematic name: 1-(5-phosphoribosyl)-ATP diphosphohydrolase

Comments: The Neurospora crassa enzyme also catalyses the reactions of EC 1.1.1.23 (histidinol dehydrogenase) and EC 3.5.4.19 (phosphoribosyl-AMP cyclohydrolase).

References: [2365]

[3.6.1.32 Transferred entry. myosin ATPase. Now EC 3.6.4.1, myosin ATPase]

[3.6.1.33 Transferred entry. dynein ATPase. Now EC 3.6.4.2, dynein ATPase]


[3.6.1.35 Transferred entry. H$^+$-transporting ATPase. Now EC 3.6.3.6, H$^+$-exporting ATPase]


[3.6.1.37 Transferred entry. Na$^+$/K$^+$ exchanging ATPase. Now EC 3.6.3.9, Na$^+$/K$^+$-exchanging ATPase]

[3.6.1.38 Transferred entry. Ca$^{2+}$-transporting ATPase. Now EC 3.6.3.8, Ca$^{2+}$-transporting ATPase]

[EC 3.6.1.29 created 1978]

[EC 3.6.1.30 created 1978]

[EC 3.6.1.31 created 1981]
EC 3.6.1.39

Accepted name: thymidine-triphosphatase
Reaction: dTTP + H₂O = dTDP + phosphate
Other name(s): thymidine triphosphate nucleotidohydrolase; dTTPase; deoxythymidine-5′-triphosphatase
Systematic name: dTTP nucleotidohydrolase
Comments: Also acts, more slowly, on dUTP and UTP.
References: [470]

[EC 3.6.1.39 created 1984]

EC 3.6.1.40

Accepted name: guanosine-5′-triphosphate,3′-diphosphate diphosphatase
Reaction: guanosine 5′-triphosphate,3′-diphosphate + H₂O = guanosine 5′-diphosphate,3′-diphosphate + phosphate
Other name(s): pppGpp 5′-phosphohydrolase; guanosine-5′-triphosphate,3′-diphosphate pyrophosphatase; guanosine pentaphosphatase; guanosine 5′-triphosphate 3′-diphosphate 5′-phosphatase; guanosine pentaphosphate phosphohydrolase
Systematic name: guanosine-5′-triphosphate,3′-diphosphate 5′-phosphohydrolase
Comments: Also hydrolyses other guanosine 5′-triphosphate derivatives with at least one unsubstituted phosphate group on the 3′-position, but not GTP, ATP or adenosine 5′-triphosphate,3′-diphosphate.
References: [923]

[EC 3.6.1.40 created 1986]

EC 3.6.1.41

Accepted name: bis(5′-nucleosyl)-tetraphosphatase (symmetrical)
Reaction: P₁,P₄-bis(5′-adenosyl) tetraphosphate + H₂O = 2 ADP
Other name(s): diadenosinetetraphosphatase (symmetrical); dinucleosidetetraphosphatase (symmetrical); symmetrical diadenosine tetraphosphate hydrolase; adenosine tetraphosphate phosphodiesterase; Ap4A hydrolase; bis(5′-adenosyl) tetraphosphate; diadenosine tetraphosphate hydrolase; diadenosine polyphosphate hydrolase; diadenosine 5′,5″″″,5′″″−P₁,P₄-tetraphosphate; diadenosinetetraphosphatase (symmetrical); 1-P₄,A-P₄-bis(5′-nucleosyl)-tetraphosphate nucleosidebisphosphohydrolase
Systematic name: P₁,P₄-bis(5′-adenosyl)-tetraphosphate nucleosidebisphosphohydrolase
Comments: Also acts on bis(5′-guanosyl) tetraphosphate and bis(5′-adenosyl) pentaphosphatase and, more slowly, on some other polyphosphates, forming a nucleoside bisphosphate as one product in all cases [cf. EC 3.6.1.17 bis(5′-nucleosyl)-tetraphosphatase (asymmetrical)].
References: [131, 891]

[EC 3.6.1.41 created 1986]

EC 3.6.1.42

Accepted name: guanosine-diphosphatase
Reaction: GDP + H₂O = GMP + phosphate
Other name(s): GDPase
Systematic name: GDP phosphohydrolase
Comments: Also acts on UDP but not on other nucleoside diphosphates and triphosphates.
References: [2074]

[EC 3.6.1.42 created 1989]

EC 3.6.1.43

Accepted name: dolichylidiphosphatase
Reaction: dolichyl diphosphate + H₂O = dolichyl phosphate + phosphate
Other name(s): dolichol diphosphatase; dolichyl pyrophosphatase; dolichyl pyrophosphate phosphatase; dolichyl diphosphate phosphohydrolase; Dol-P-P phosphohydrolase
Systematic name: dolichyl-diphosphate phosphohydrolase
References: [1785]

[EC 3.6.1.43 created 1989]

EC 3.6.1.44
Accepted name: oligosaccharide-diphosphodolichol diphosphatase
Reaction: oligosaccharide-diphosphodolichol + H₂O = oligosaccharide phosphate + dolichyl phosphate
Other name(s): oligosaccharide-diphosphodolichol pyrophosphatase
Systematic name: oligosaccharide-diphosphodolichol phosphodolichohydrolase
References: [167]

[EC 3.6.1.44 created 1992]

EC 3.6.1.45
Accepted name: UDP-sugar diphosphatase
Reaction: UDP-sugar + H₂O = UMP + α-D-aldose 1-phosphate
Other name(s): nucleosidediphosphate-sugar pyrophosphatase; nucleosidediphosphate-sugar diphosphatase; UDP-sugar hydrolase; UDP-sugar pyrophosphatase
Systematic name: UDP-sugar sugarphosphohydrolase
Comments: A divalent cation is required for activity. UDP-sugar is the best substrate, although other nucleoside-sugar diphosphates are used as substrates with similar \( K_m \) values but much lower maximum velocities. Thus, this enzyme has a specificity distinct from that of ADP-sugar diphosphatase (EC 3.6.1.21). Some but not all enzymes of this class also appear to have 5′-nucleotidase (see EC 3.1.3.5) activity.
References: [784, 823]

[EC 3.6.1.45 created 1999]

[3.6.1.46 Transferred entry. heterotrimeric G-protein GTPase. Now EC 3.6.5.1, heterotrimeric G-protein GTPase]

[EC 3.6.1.46 created 2000, deleted 2003]

[3.6.1.47 Transferred entry. small monomeric GTPase. Now EC 3.6.5.2, small monomeric GTPase]

[EC 3.6.1.47 created 2000, deleted 2003]

[3.6.1.48 Transferred entry. protein-synthesizing GTPase. Now EC 3.6.5.3, protein-synthesizing GTPase]

[EC 3.6.1.48 created 2000, deleted 200]

[3.6.1.49 Transferred entry. signal-recognition-particle GTPase. Now EC 3.6.5.4, signal-recognition-particle GTPase]

[EC 3.6.1.49 created 2000, deleted 2003]

[3.6.1.50 Transferred entry. dynamin GTPase. Now EC 3.6.5.5, dynamin GTPase]

[EC 3.6.1.50 created 2000, deleted 2003]

[3.6.1.51 Transferred entry. tubulin GTPase. Now EC 3.6.5.6, tubulin GTPase]

[EC 3.6.1.51 created 2000, deleted 2003]

EC 3.6.1.52
Accepted name: diphosphoinositol-polyporphosphate diphosphatase
Reaction: diphospho-myoinositol polyphosphate + H₂O = myo-inositol polyphosphate + phosphate

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Other name(s): diphosphoinositol-polyphosphate phosphohydrolase; DIPP
Systematic name: diphospho-myoinositol-polyphosphate diphosphohydrolase
Comments: This enzyme hydrolyses the diphosphate bond, leaving a phospho group where a diphospho group had been. It can also act on bis(adenosine) diphosphate.
References: [2177, 322]

EC 3.6.1.53
Accepted name: Mn^{2+}-dependent ADP-ribose/CDP-alcohol diphosphatase
Reaction: (1) CDP-choline + H_2O = CMP + phosphocholine
(2) ADP-ribose + H_2O = AMP + D-ribose 5-phosphate
Other name(s): Mn^{2+}-dependent ADP-ribose/CDP-alcohol pyrophosphatase; ADP-Ribase-Mn
Systematic name: CDP-choline phosphohydrolase
Comments: Requires Mn^{2+}, which cannot be replaced by Mg^{2+}, for activity. ADP-ribose, CDP-choline, CDP-ethanolamine and ADP are substrates for this enzyme but ADP-glucose, UDP-glucose, CDP-glucose, CDP, CMP and AMP are not hydrolysed [332]. In rat, the enzyme is found predominantly in thymus and spleen.
References: [333, 332]

EC 3.6.1.54
Accepted name: UDP-2,3-diacylglucosamine diphosphatase
Reaction: UDP-2,3-bis[(3R)-3-hydroxymyristoyl]-α-D-glucosamine + H_2O = 2,3-bis[(3R)-3-hydroxymyristoyl]-β-D-glucosaminyl 1-phosphate + UMP
Other name(s): UDP-2,3-diacylglucosamine hydrolase; UDP-2,3-diacylglucosamine pyrophosphatase; ybbF (gene name); lpxH (gene name)
Systematic name: UDP-2,3-bis[(3R)-3-hydroxymyristoyl]-α-D-glucosamine 2,3-bis[(3R)-3-hydroxymyristoyl]-β-D-glucosaminyl 1-phosphate phosphohydrolase
Comments: The enzyme catalyses a step in the biosynthesis of lipid A.
References: [96, 95]

EC 3.6.2 In sulfonyl-containing anhydrides

EC 3.6.2.1
Accepted name: adenylysulfatase
Reaction: adenylyl sulfate + H_2O = AMP + sulfate
Other name(s): adenosine 5-phosphosulfate sulfohydrolase; adenylysulfate sulfohydrolase
Systematic name: adenylyl-sulfate sulfohydrolase
References: [108]

EC 3.6.2.2
Accepted name: phosphoadenylylsulfatase
Reaction: 3'-phosphoadenylyl sulfate + H_2O = adenosine 3',5'-bisphosphate + sulfate
Other name(s): 3-phosphoadenylyl sulfae; 3-phosphoadenosine 5-phosphosulfate sulfatase; PAPS sulfatase; 3'-phosphoadenylylsulfate sulfohydrolase
Systematic name: 3'-phosphoadenylyl-sulfate sulfohydrolase
EC 3.6.3 Acting on acid anhydrides to catalyse transmembrane movement of substances

Several types of ATP phosphohydrolase are listed here. Entries EC 3.6.3.1 to EC 3.6.3.12 and EC 3.6.3.53 are enzymes undergoing covalent phosphorylation of an aspartate residue during the transport cycle; entries EC 3.6.3.14 and EC 3.6.3.15 refer to enzymes of complicated membrane and non-membrane location that can also serve in ATP synthesis; entry EC 3.6.3.16 is a multisubunit enzyme that is involved in arsenite transport only; entries EC 3.6.3.17 to EC 3.6.3.50 are two-domain enzymes of the ABC family; entries EC 3.6.3.51 and EC 3.6.3.52 are parts of a complex protein-transporting machinery in mitochondria and chloroplasts.

EC 3.6.3.1

Accepted name: phospholipid-translocating ATPase
Reaction: \( \text{ATP} + \text{H}_2\text{O} + \text{phospholipid}_{in} = \text{ADP} + \text{phosphate} + \text{phospholipid}_{out} \)
Other name(s): Mg\(^{2+}\)-ATPase; flippase; aminophospholipid-transporting ATPase
Systematic name: ATP phosphohydrolase (phospholipid-flipping)
Comments: A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. The enzyme apparently has several activities, one of them being the movement of phospholipids from one membrane face to the other (‘flippase’).
References: [1716, 2691, 2459, 88]

EC 3.6.3.2

Accepted name: Mg\(^{2+}\)-importing ATPase
Reaction: \( \text{ATP} + \text{H}_2\text{O} + \text{Mg}^{2+}_{out} = \text{ADP} + \text{phosphate} + \text{Mg}^{2+}_{in} \)
Systematic name: ATP phosphohydrolase (Mg\(^{2+}\)-importing)
Comments: A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. This enzyme occurs in both Gram-positive and Gram-negative bacteria, and three types are known, designated as CorA, MgtA and MgtB. The CorA itself is not an ATPase but an Mg\(^{2+}\) transporter.
References: [2526, 2368]

EC 3.6.3.3

Accepted name: Cd\(^{2+}\)-exporting ATPase
Reaction: \( \text{ATP} + \text{H}_2\text{O} + \text{Cd}^{2+}_{in} = \text{ADP} + \text{phosphate} + \text{Cd}^{2+}_{out} \)
Systematic name: ATP phosphohydrolase (Cd\(^{2+}\)-exporting)
Comments: A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. This enzyme occurs in protozoa, fungi and plants.
References: [2327, 2598]

EC 3.6.3.4

Accepted name: Cu\(^{2+}\)-exporting ATPase
Reaction: \( \text{ATP} + \text{H}_2\text{O} + \text{Cu}^{2+}_{in} = \text{ADP} + \text{phosphate} + \text{Cu}^{2+}_{out} \)
Systematic name: ATP phosphohydrolase (Cu\(^{2+}\)-exporting)
Comments: A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. This bacterial and mammalian enzyme exports Cu\(^{2+}\) from cells. In humans, it is involved in Menkes disease and Wilson’s disease.
**EC 3.6.3.5**

**Accepted name:** Zn\(^{2+}\)-exporting ATPase  
**Reaction:** \(\text{ATP} + \text{H}_2\text{O} + \text{Zn}^{2+}_{\text{in}} = \text{ADP} + \text{phosphate} + \text{Zn}^{2+}_{\text{out}}\)  
**Other name(s):** Zn(II)-translocating P-type ATPase; P1B-type ATPase; AtHMA4  
**Systematic name:** ATP phosphohydrolase (Zn\(^{2+}\)-exporting)  
**Comments:** A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. This enzyme also exports Cd\(^{2+}\) and Pb\(^{2+}\).  
**References:** [159, 2097, 2098, 1665, 636]  

**EC 3.6.3.6**

**Accepted name:** H\(^{+}\)-exporting ATPase  
**Reaction:** \(\text{ATP} + \text{H}_2\text{O} + \text{H}^{+}_{\text{in}} = \text{ADP} + \text{phosphate} + \text{H}^{+}_{\text{out}}\)  
**Other name(s):** proton-translocating ATPase; yeast plasma membrane H\(^{+}\)-ATPase; yeast plasma membrane ATPase; ATP phosphohydrolase  
**Systematic name:** ATP phosphohydrolase (H\(^{+}\)-exporting)  
**Comments:** A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. This enzyme occurs in protozoa, fungi and plants, and generates an electrochemical potential gradient of protons across the plasma membrane.  
**References:** [833, 2280, 2281]  

**EC 3.6.3.7**

**Accepted name:** Na\(^{+}\)-exporting ATPase  
**Reaction:** \(\text{ATP} + \text{H}_2\text{O} + \text{Na}^{+}_{\text{in}} = \text{ADP} + \text{phosphate} + \text{Na}^{+}_{\text{out}}\)  
**Systematic name:** ATP phosphohydrolase (Na\(^{+}\)-exporting)  
**Comments:** A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. This enzyme from yeast is involved in the efflux of Na\(^{+}\), with one ion being exported per ATP hydrolysed.  
**References:** [2796, 348, 384, 2180]  

**EC 3.6.3.8**

**Accepted name:** Ca\(^{2+}\)-transporting ATPase  
**Reaction:** \(\text{ATP} + \text{H}_2\text{O} + \text{Ca}^{2+}_{\text{cis}} = \text{ADP} + \text{phosphate} + \text{Ca}^{2+}_{\text{trans}}\)  
**Other name(s):** sarcoplasmic reticulum ATPase; sarco(endo)plasmic reticulum Ca\(^{2+}\)-ATPase; calcium pump; Ca\(^{2+}\)-pumping ATPase; plasma membrane Ca-ATPase  
**Systematic name:** ATP phosphohydrolase (Ca\(^{2+}\)-transporting)  
**Comments:** A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. This enzyme family comprises three types of Ca\(^{2+}\)-transporting enzymes that are found in the plasma membrane, the sarcoplasmic reticulum and in yeast. The first and third transport one ion per ATP hydrolysed, whereas the second transports two ions.  
**References:** [2232, 1089, 337, 1525]  

**References:** [2707, 1967, 1686]  

[EC 3.6.3.4 created 2000]  

[EC 3.6.3.5 created 2000, modified 2001, modified 2006]  

[EC 3.6.3.6 created 1984 as EC 3.6.1.35, transferred 2000 to EC 3.6.3.6]  

[EC 3.6.3.7 created 2000, modified 2001]  

[EC 3.6.3.8 created 1984 as EC 3.6.1.38, transferred 2000 to EC 3.6.3.8, modified 2001]
EC 3.6.3.9

**Accepted name:** Na\(^+\)/K\(^+\)-exchanging ATPase  
**Reaction:** ATP + H\(_2\)O + Na\(^{in}\) + K\(^+\)\(_{out}\) = ADP + phosphate + Na\(^{out}\) + K\(^+\)\(_{in}\)  
**Systematic name:** ATP phosphohydrolase (Na\(^+\)/K\(^+\)-exchanging)  
**Comments:** A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. This is a plasma membrane enzyme, ubiquitous in animal cells, that catalyses the efflux of three Na\(^+\) and influx of two K\(^+\) per ATP hydrolysed. It is involved in generating the plasma membrane electrical potential.

**References:** [2353, 2008, 2354]

[EC 3.6.3.9 created 1984 as EC 3.6.1.37, transferred 2000 to EC 3.6.3.9, modified 2001]

EC 3.6.3.10

**Accepted name:** H\(^+\)/K\(^+\)-exchanging ATPase  
**Reaction:** ATP + H\(_2\)O + H\(^+\)\(_{in}\) + K\(^+\)\(_{out}\) = ADP + phosphate + H\(^+\)\(_{out}\) + K\(^+\)\(_{in}\)  
**Other name(s):** H\(^+\)-K\(^+\)-ATPase; H,K-ATPase; (K\(^+\)+H\(^+\))-ATPase  
**Systematic name:** ATP phosphohydrolase (H\(^+\)/K\(^+\)-exchanging)  
**Comments:** A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. A gastric mucosal enzyme that catalyses the efflux of one H\(^+\) and the influx of one K\(^+\) per ATP hydrolysed.

**References:** [2172, 998, 2036]

[EC 3.6.3.10 created 1984 as EC 3.6.1.36, transferred 2000 to EC 3.6.3.10]

EC 3.6.3.11

**Accepted name:** Cl\(^-\)-transporting ATPase  
**Reaction:** ATP + H\(_2\)O + Cl\(^-\)\(_{out}\) = ADP + phosphate + Cl\(^-\)\(_{in}\)  
**Other name(s):** Cl\(^-\)-translocating ATPase; Cl\(^-\)-motive ATPase  
**Systematic name:** ATP phosphohydrolase (Cl\(^-\)-importing)  
**Comments:** A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. An animal and plant enzyme involved in the import of chloride anions.

**References:** [1873, 797, 1085]

[EC 3.6.3.11 created 2000]

EC 3.6.3.12

**Accepted name:** K\(^+\)-transporting ATPase  
**Reaction:** ATP + H\(_2\)O + K\(^+\)\(_{out}\) = ADP + phosphate + K\(^+\)\(_{in}\)  
**Other name(s):** K\(^+\)-translocating Kdp-ATPase; multi-subunit K\(^+\)-transport ATPase  
**Systematic name:** ATP phosphohydrolase (K\(^+\)-importing)  
**Comments:** A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. A bacterial enzyme of di(heterotetrameric) structure that is involved in K\(^+\) import. The probable stoichiometry is one ion per ATP hydrolysed.

**References:** [2321, 785]

[EC 3.6.3.12 created 2000]

EC 3.6.3.13

*Deleted entry.* aminophospholipid-transporting ATPase. Identical to EC 3.6.3.1, phospholipid-translocating ATPase.

[EC 3.6.3.13 created 2000, deleted 2001]

EC 3.6.3.14

**Accepted name:** H\(^+\)-transporting two-sector ATPase  
**Reaction:** ATP + H\(_2\)O + H\(^+\)\(_{in}\) = ADP + phosphate + H\(^+\)\(_{out}\)
Other name(s): ATP synthase; F₁-F₄-ATPase; H⁺-transporting ATPase; mitochondrial ATPase; coupling factors (F₀, F₁ and CF₁); chloroplast ATPase; bacterial Ca²⁺/Mg²⁺ ATPase

Systematic name: ATP phosphohydrolase (H⁺-transporting)

Comments: A multisubunit non-phosphorylated ATPase that is involved in the transport of ions. Large enzymes of mitochondria, chloroplasts and bacteria with a membrane sector (F₀, V₀, A₀) and a cytoplasmic-compartment sector (F₁, V₁, A₁). The F-type enzymes of the inner mitochondrial and thylakoid membranes act as ATP synthases. All of the enzymes included here operate in a rotational mode, where the extramembrane sector (containing 3 α- and 3 β-subunits) is connected via the δ-subunit to the membrane sector by several smaller subunits. Within this complex, the γ- and ε-subunits, as well as the 9-12 c subunits rotate by consecutive 120° angles and perform parts of ATP synthesis. This movement is driven by the H⁺ electrochemical potential gradient. The V-type (in vacuoles and clathrin-coated vesicles) and A-type (archebacterial) enzymes have a similar structure but, under physiological conditions, they pump H⁺ rather than synthesize ATP.

References: [250, 8, 211, 1823]

[EC 3.6.3.14 created 1984 as EC 3.6.1.34, transferred 2000 to EC 3.6.3.14]

EC 3.6.3.15

Accepted name: Na⁺-transporting two-sector ATPase

Reaction: ATP + H₂O + Na⁺₂ in = ADP + phosphate + Na⁺₂ out

Systematic name: ATP phosphohydrolase (Na⁺-transporting)

Comments: A multisubunit non-phosphorylated ATPase that is involved in the transport of ions. An enzyme found in alkaliphilic bacteria that is similar to EC 3.6.3.14 (H⁺-transporting two-sector ATPase) where Na⁺ replaces H⁺.

References: [2381, 2497, 2043]

[EC 3.6.3.15 created 2000]

EC 3.6.3.16

Accepted name: arsenite-transporting ATPase

Reaction: ATP + H₂O + arsenite in = ADP + phosphate + arsenite out

Systematic name: ATP phosphohydrolase (arsenite-exporting)

Comments: A multisubunit non-phosphorylated ATPase that is involved in the transport of ions. A bacterial enzyme that usually contains two subunits where one (with 12 membrane-spanning segments) forms the ‘channel’ part and the other (occurring in pairs peripherally to the membrane) contains the ATP-binding site. Exports arsenite and antimonite anions.

References: [2328, 2146, 293, 2920]

[EC 3.6.3.16 created 2000]

EC 3.6.3.17

Accepted name: monosaccharide-transporting ATPase

Reaction: ATP + H₂O + monosaccharide in = ADP + phosphate + monosaccharide out

Systematic name: ATP phosphohydrolase (monosaccharide-importing)

Comments: ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. Family of bacterial enzymes importing ribose, xylose, arabinose, galactose and methylgalactoside.

References: [1005, 1336, 1229, 2180, 2385, 869]

[EC 3.6.3.17 created 2000]

EC 3.6.3.18

Accepted name: oligosaccharide-transporting ATPase

References: [1005, 1336, 1229, 2180, 2385, 869]
Reaction: \( \text{ATP} + H_2O + \text{oligosaccharide}_{out} = \text{ADP} + \text{phosphate} + \text{oligosaccharide}_{in} \)

Systematic name: ATP phosphohydrolase (disaccharide-importing)

Comments: ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports lactose, melibiose and raffinose.

References: [1005, 1336, 2031, 2180, 2805]

[EC 3.6.3.18 created 2000]

EC 3.6.3.19

Accepted name: maltose-transporting ATPase

Reaction: \( \text{ATP} + H_2O + \text{maltose}_{out} = \text{ADP} + \text{phosphate} + \text{maltose}_{in} \)

Systematic name: ATP phosphohydrolase (maltose-importing)

Comments: ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. Comprises bacterial enzymes that import maltose and maltose oligosaccharides.

References: [1005, 480, 1336, 2180, 869]

[EC 3.6.3.19 created 2000]

EC 3.6.3.20

Accepted name: glycerol-3-phosphate-transporting ATPase

Reaction: \( \text{ATP} + H_2O + \text{glycerol-3-phosphate}_{out} = \text{ADP} + \text{phosphate} + \text{glycerol-3-phosphate}_{in} \)

Systematic name: ATP phosphohydrolase (glycerol-3-phosphate-importing)

Comments: ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports phosphorylated glycerol.

References: [2180, 869, 103]

[EC 3.6.3.20 created 2000]

EC 3.6.3.21

Accepted name: polar-amino-acid-transporting ATPase

Reaction: \( \text{ATP} + H_2O + \text{polar amino acid}_{out} = \text{ADP} + \text{phosphate} + \text{polar amino acid}_{in} \)

Other name(s): histidine permease

Systematic name: ATP phosphohydrolase (polar-amino-acid-importing)

Comments: ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. Comprises bacterial enzymes that import His, Arg, Lys, Glu, Gln, Asp, ornithine, octopine and nopaline.

References: [1336, 2180, 1808, 2727]

[EC 3.6.3.21 created 2000]

EC 3.6.3.22

Accepted name: nonpolar-amino-acid-transporting ATPase

Reaction: \( \text{ATP} + H_2O + \text{nonpolar amino acid}_{out} = \text{ADP} + \text{phosphate} + \text{nonpolar amino acid}_{in} \)

Systematic name: ATP phosphohydrolase (nonpolar-amino-acid-importing)

Comments: ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. Comprises bacterial enzymes that import Leu, Ile and Val.

References: [1336, 2180, 869]

[EC 3.6.3.22 created 2000]

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EC 3.6.3.23
**Accepted name:** oligopeptide-transporting ATPase  
**Reaction:** \( \text{ATP} + H_2O + \text{oligopeptide}_{out} = \text{ADP} + \text{phosphate} + \text{oligopeptide}_{in} \)  
**Other name(s):** oligopeptide permease  
**Systematic name:** ATP phosphohydrolase (oligopeptide-importing)  
**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports di- and oligopeptides.  
**References:** [1336, 2180, 869, 1953]

[EC 3.6.3.23 created 2000]

EC 3.6.3.24
**Accepted name:** nickel-transporting ATPase  
**Reaction:** \( \text{ATP} + H_2O + \text{Ni}^{2+}_{out} = \text{ADP} + \text{phosphate} + \text{Ni}^{2+}_{in} \)  
**Systematic name:** ATP phosphohydrolase (nickel-importing)  
**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports \( \text{Ni}^{2+} \).  
**References:** [1336, 980, 2180, 869]

[EC 3.6.3.24 created 2000]

EC 3.6.3.25
**Accepted name:** sulfate-transporting ATPase  
**Reaction:** \( \text{ATP} + H_2O + \text{sulfate}_{out} = \text{ADP} + \text{phosphate} + \text{sulfate}_{in} \)  
**Systematic name:** ATP phosphohydrolase (sulfate-importing)  
**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports sulfate and thiosulfate anions.  
**References:** [2342, 1336, 2180]

[EC 3.6.3.25 created 2000]

EC 3.6.3.26
**Accepted name:** nitrate-transporting ATPase  
**Reaction:** \( \text{ATP} + H_2O + \text{nitrate}_{out} = \text{ADP} + \text{phosphate} + \text{nitrate}_{in} \)  
**Systematic name:** ATP phosphohydrolase (nitrate-importing)  
**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports \( \text{NO}_3^- \), \( \text{NO}_2^- \) and \( \text{OCN}^- \).  
**References:** [1902, 1336, 2180, 869]

[EC 3.6.3.26 created 2000]

EC 3.6.3.27
**Accepted name:** phosphate-transporting ATPase  
**Reaction:** \( \text{ATP} + H_2O + \text{phosphate}_{out} = \text{ADP} + \text{phosphate} + \text{phosphate}_{in} \)  
**Other name(s):** ABC phosphate transporter  
**Systematic name:** ATP phosphohydrolase (phosphate-importing)  
**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports phosphate anions.  
**References:** [2759, 1336, 254, 2180, 869]
EC 3.6.3.28

**Accepted name:** phosphonate-transporting ATPase  
**Reaction:** $\text{ATP} + \text{H}_2\text{O} + \text{phosphonate}_{\text{out}} = \text{ADP} + \text{phosphate} + \text{phosphonate}_{\text{in}}$  
**Systematic name:** ATP phosphohydrolase (phosphonate-transporting)  
**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports phosphonate and organophosphate anions.  
**References:** [2743, 1336, 2180, 869]

EC 3.6.3.29

**Accepted name:** molybdate-transporting ATPase  
**Reaction:** $\text{ATP} + \text{H}_2\text{O} + \text{molybdate}_{\text{out}} = \text{ADP} + \text{phosphate} + \text{molybdate}_{\text{in}}$  
**Systematic name:** ATP phosphohydrolase (molybdate-importing)  
**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports molybdate anions.  
**References:** [1336, 883, 2180, 869]

EC 3.6.3.30

**Accepted name:** Fe$^{3+}$-transporting ATPase  
**Reaction:** $\text{ATP} + \text{H}_2\text{O} + \text{Fe}^{3+}_{\text{out}} = \text{ADP} + \text{phosphate} + \text{Fe}^{3+}_{\text{in}}$  
**Systematic name:** ATP phosphohydrolase (ferric-ion-transporting)  
**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports ferric cations.  
**References:** [53, 1336, 2180, 1246]

EC 3.6.3.31

**Accepted name:** polyamine-transporting ATPase  
**Reaction:** $\text{ATP} + \text{H}_2\text{O} + \text{polyamine}_{\text{out}} = \text{ADP} + \text{phosphate} + \text{polyamine}_{\text{in}}$  
**Systematic name:** ATP phosphohydrolase (polyamine-importing)  
**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports putrescine and spermidine.  
**References:** [1206, 1336, 2180]

EC 3.6.3.32

**Accepted name:** quaternary-amine-transporting ATPase  
**Reaction:** $\text{ATP} + \text{H}_2\text{O} + \text{quaternary amine}_{\text{out}} = \text{ADP} + \text{phosphate} + \text{quaternary amine}_{\text{in}}$  
**Systematic name:** ATP phosphohydrolase (quaternary-amine-importing)  
**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports betaine and glycine.
EC 3.6.3.33

Accepted name: vitamin B\textsubscript{12}-transporting ATPase

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{vitamin B}_{12}\text{out} = \text{ADP} + \text{phosphate} + \text{vitamin B}_{12}\text{in}$

Systematic name: ATP phosphohydrolase (vitamin B\textsubscript{12}-importing)

Comments: ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports cobalamin derivatives.

References: [1336, 2180, 736]

[EC 3.6.3.33 created 2000]

EC 3.6.3.34

Accepted name: iron-chelate-transporting ATPase

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{iron chelate}_{\text{out}} = \text{ADP} + \text{phosphate} + \text{iron chelate}_{\text{in}}$

Systematic name: ATP phosphohydrolase (iron-chelate-importing)

Comments: ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports Fe-enterobactin, Fe-dicitrate, Fe-hydroxamate and other siderophores.

References: [2295, 1315, 1336, 2180, 1526]

[EC 3.6.3.34 created 2000]

EC 3.6.3.35

Accepted name: manganese-transporting ATPase

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{Mn}^{2+}_{\text{out}} = \text{ADP} + \text{phosphate} + \text{Mn}^{2+}_{\text{in}}$

Other name(s): ABC-type manganese permease complex

Systematic name: ATP phosphohydrolase (manganese-importing)

Comments: ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports Mn\textsuperscript{2+}, Zn\textsuperscript{2+} and iron chelates.

References: [1336, 2180, 1836, 1300]

[EC 3.6.3.35 created 2000]

EC 3.6.3.36

Accepted name: taurine-transporting ATPase

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{taurine}_{\text{out}} = \text{ADP} + \text{phosphate} + \text{taurine}_{\text{in}}$

Systematic name: ATP phosphohydrolase (taurine-importing)

Comments: ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports taurine.

References: [2670]

[EC 3.6.3.36 created 2000]

EC 3.6.3.37

Accepted name: guanine-transporting ATPase

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{guanine}_{\text{out}} = \text{ADP} + \text{phosphate} + \text{guanine}_{\text{in}}$

References: [2670]

[EC 3.6.3.37 created 2000]
**Systematic name:** ATP phosphohydrolase (guanine-importing)

**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A eukaryotic enzyme that imports guanine and tryptophan (it contains a single ATP-binding site).

**References:** [580, 2536, 869]

[EC 3.6.3.37 created 2000]

**EC 3.6.3.38**

**Accepted name:** capsular-polysaccharide-transporting ATPase

**Reaction:** ATP + H₂O + capsular polysaccharide_{in} = ADP + phosphate + capsular polysaccharide_{out}

**Systematic name:** ATP phosphohydrolase (capsular-polysaccharide-exporting)

**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. An enzyme that exports capsular polysaccharide from Gram-negative bacteria.

**References:** [666, 1948, 1979, 2180, 869]

[EC 3.6.3.38 created 2000]

**EC 3.6.3.39**

**Accepted name:** lipopolysaccharide-transporting ATPase

**Reaction:** ATP + H₂O + lipopolysaccharide_{in} = ADP + phosphate + lipopolysaccharide_{out}

**Systematic name:** ATP phosphohydrolase (lipopolysaccharide-exporting)

**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. Enzymes of Gram-negative bacteria that export lipo-oligosaccharides and lipopolysaccharides.

**References:** [666, 678, 1948, 2180]

[EC 3.6.3.39 created 2000]

**EC 3.6.3.40**

**Accepted name:** teichoic-acid-transporting ATPase

**Reaction:** ATP + H₂O + teichoic acid_{in} = ADP + phosphate + teichoic acid_{out}

**Systematic name:** ATP phosphohydrolase (teichoic-acid-exporting)

**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. An enzyme found in Gram-positive bacteria that exports teichoic acid.

**References:** [666, 1389, 1948, 869]

[EC 3.6.3.40 created 2000]

**EC 3.6.3.41**

**Accepted name:** heme-transporting ATPase

**Reaction:** ATP + H₂O + heme_{in} = ADP + phosphate + heme_{out}

**Systematic name:** ATP phosphohydrolase (heme-exporting)

**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. An enzyme found in Gram-negative bacteria that exports heme.

**References:** [2180, 1138, 2054]

[EC 3.6.3.41 created 2000]
**EC 3.6.3.42**

**Accepted name:** β-glucan-transporting ATPase

**Reaction:** $\text{ATP} + \text{H}_2\text{O} + \beta$-glucan$_{\text{in}} = \text{ADP} + \text{phosphate} + \beta$-glucan$_{\text{out}}$

**Systematic name:** ATP phosphohydrolase (β-glucan-exporting)

**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. An enzyme found in Gram-negative bacteria that exports β-glucan.

**References:** [666, 161, 2180, 869]

[EC 3.6.3.42 created 2000]

**EC 3.6.3.43**

**Accepted name:** peptide-transporting ATPase

**Reaction:** $\text{ATP} + \text{H}_2\text{O} + \text{peptide}_{\text{in}} = \text{ADP} + \text{phosphate} + \text{peptide}_{\text{out}}$

**Systematic name:** ATP phosphohydrolase (peptide-exporting)

**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A family of enzymes that exports α-hemolysin, cyclolysin, colicin V and siderophores from Gram-negative bacteria, and bacteriocin, subtilin, competence factor and pediocin from Gram-positive bacteria.

**References:** [1280, 1692, 195]

[EC 3.6.3.43 created 2000]

**EC 3.6.3.44**

**Accepted name:** xenobiotic-transporting ATPase

**Reaction:** $\text{ATP} + \text{H}_2\text{O} + \text{xenobiotic}_{\text{in}} = \text{ADP} + \text{phosphate} + \text{xenobiotic}_{\text{out}}$

**Other name(s):** multidrug-resistance protein; MDR protein; P-glycoprotein; pleiotropic-drug-resistance protein; PDR protein; steroid-transporting ATPase; ATP phosphohydrolase (steroid-exporting)

**Systematic name:** ATP phosphohydrolase (xenobiotic-exporting)

**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. The enzyme from Gram-positive bacteria and eukaryotic cells export a number of drugs, with unusual specificity, covering various groups of unrelated substances, while ignoring some that are closely related structurally. Several distinct enzymes may be present in a single eukaryotic cell. Many of them transport glutathione—drug conjugates. Some also show some ‘flipase’ (phospholipid-translocating ATPase; EC 3.6.3.1) activity.

**References:** [169, 737, 1231, 1492, 2678, 869, 2017, 1751, 1531]

[EC 3.6.3.44 created 2000 (EC 3.6.3.45 incorporated 2006), modified 2006]

[3.6.3.45 Deleted entry. steroid-transporting ATPase. Now included with EC 3.6.3.44, xenobiotic-transporting ATPase]

[EC 3.6.3.45 created 2000, deleted 2006]

**EC 3.6.3.46**

**Accepted name:** cadmium-transporting ATPase

**Reaction:** $\text{ATP} + \text{H}_2\text{O} = \text{ADP} + \text{phosphate}$

**Systematic name:** ATP phosphohydrolase (heavy-metal-exporting)

**Comments:** ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A yeast enzyme that exports some heavy metals, especially Cd$^{2+}$, from the cytosol into the vacuole.

**References:** [1449, 2180]

[EC 3.6.3.46 created 2000]
EC 3.6.3.47

Accepted name: fatty-acyl-CoA-transporting ATPase
Reaction: ATP + H₂O + fatty acyl CoA<sub>cis</sub> = ADP + phosphate + fatty acyl CoA<sub>trans</sub>
Systematic name: ATP phosphohydrolase (fatty-acyl-CoA-transporting)
Comments: ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. An animal and yeast enzyme that transports fatty acyl CoA into and out of peroxisomes. In humans, it is associated with Zellweger's syndrome.
References: [1188, 1002, 2180]

[EC 3.6.3.47 created 2000]

EC 3.6.3.48

Accepted name: α-factor-transporting ATPase
Reaction: ATP + H₂O + α-factor<sub>in</sub> = ADP + phosphate + α-factor<sub>out</sub>
Systematic name: ATP phosphohydrolase (α-factor-transporting)
Comments: ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. A yeast enzyme that exports the α-factor sex pheromone.
References: [1649, 2180]

[EC 3.6.3.48 created 2000]

EC 3.6.3.49

Accepted name: channel-conductance-controlling ATPase
Reaction: ATP + H₂O = ADP + phosphate
Systematic name: ATP phosphohydrolase (channel-conductance-controlling)
Comments: ABC-type (ATP-binding cassette-type) ATPase, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. An animal enzyme that is active in forming a chloride channel, the absence of which brings about cystic fibrosis. It is also involved in the functioning of other transmembrane channels.
References: [375, 2633, 2298]

[EC 3.6.3.49 created 2000]

EC 3.6.3.50

Accepted name: protein-secreting ATPase
Reaction: ATP + H₂O = ADP + phosphate
Systematic name: ATP phosphohydrolase (protein-secreting)
Comments: A non-phosphorylated, non-ABC (ATP-binding cassette) ATPase that is involved in protein transport. There are several families of enzymes included here, e.g. ATP-hydrolysing enzymes of the general secretory pathway (Sec or Type II), of the virulence-related secretory pathway (Type III) and of the conjugal DNA-protein transfer pathway (Type IV). Type II enzymes occur in bacteria, archaea and eucarya, whereas type III and type IV enzymes occur in bacteria where they form components of a multi-subunit complex.
References: [2179, 1627, 2552, 110, 1576, 2260]

[EC 3.6.3.50 created 2000]

EC 3.6.3.51

Accepted name: mitochondrial protein-transporting ATPase
Reaction: ATP + H₂O = ADP + phosphate
Systematic name: ATP phosphohydrolase (mitochondrial protein-importing)
Comments: A non-phosphorylated, non-ABC (ATP-binding cassette) ATPase involved in the transport of proteins or preproteins into mitochondria using the TIM protein complex. (TIM is the protein transport machinery of the inner mitochondrial membrane that contains three essential Tim proteins: Tim17 and Tim23 are thought to build a preprotein translocation channel while Tim44 interacts transiently with the matrix heat-shock protein Hsp70 to form an ATP-driven import motor.)

References: [235, 183, 2706]

[EC 3.6.3.51 created 2000]

EC 3.6.3.52

Accepted name: chloroplast protein-transporting ATPase
Reaction: ATP + H₂O = ADP + phosphate
Systematic name: ATP phosphohydrolase (chloroplast protein-importing)
Comments: A non-phosphorylated, non-ABC (ATP-binding cassette) ATPase that is involved in protein transport. Involved in the transport of proteins or preproteins into chloroplast stroma (several ATPases may participate in this process).
References: [415, 1767, 2268]

[EC 3.6.3.52 created 2000]

EC 3.6.3.53

Accepted name: Ag⁺-exporting ATPase
Reaction: ATP + H₂O + Ag⁺ₜₐ₅ = ADP + phosphate + Ag⁺ₙₐ₅
Systematic name: ATP phosphohydrolase (Ag⁺-exporting)
Comments: A P-type ATPase that exports Ag⁺ ions from pathogenic microorganisms as well as from some animal tissues.
References: [890, 305]

[EC 3.6.3.53 created 2000]

EC 3.6.4 Acting on acid anhydrides to facilitate cellular and subcellular movement

EC 3.6.4.1

Accepted name: myosin ATPase
Reaction: ATP + H₂O = ADP + phosphate
Systematic name: ATP phosphohydrolase (actin-translocating)
Comments: Proteins of the contractile apparatus of muscle and nonmuscle cells; myosin molecule consists of two heavy chains (about 200 kDa) and two pairs of light chains (15-27 kDa). The head region of the heavy chain contains actin- and ATP-binding sites. ATP hydrolysis provides energy for actomyosin contraction.
References: [2075, 945, 1739]

[EC 3.6.4.1 created 1984 as EC 3.6.1.32, transferred 2000 to EC 3.6.4.1]

EC 3.6.4.2

Accepted name: dynein ATPase
Reaction: ATP + H₂O = ADP + phosphate
Other name(s): dynein adenosine 5'-triphosphatase
Systematic name: ATP phosphohydrolase (tubulin-translocating)
Comments: A multisubunit protein complex associated with microtubules. Hydrolysis of ATP provides energy for the movement of organelles (endosomes, lysosomes, mitochondria) along microtubules to the centrosome towards the microtubule’s minus end. It also functions in the movement of eukaryotic flagella and cilia. It consists of two heavy chains (about 500 kDa), three-four intermediate chains (about 70 kDa) and four light chains (about 50 kDa).

References: [2447, 808, 789]

[EC 3.6.4.2 created 1984 as EC 3.6.1.33, transferred 2000 to EC 3.6.4.2]

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EC 3.6.4.3

Accepted name: microtubule-severing ATPase

Reaction: ATP + H₂O = ADP + phosphate

Systematic name: ATP phosphohydrolase (tubulin-dimerizing)

Comments: Another member of the AAA-ATPase family, active in splitting microtubules into tubulin dimers in the centrosome.

References: [1624, 938]

[EC 3.6.4.3 created 2000]

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EC 3.6.4.4

Accepted name: plus-end-directed kinesin ATPase

Reaction: ATP + H₂O = ADP + phosphate

Other name(s): kinesin

Systematic name: kinesin ATP phosphohydrolase (plus-end-directed)

Comments: Microtubular motor protein, involved in organelle movement, in mitosis and meiosis. In contrast to dynein, it moves along microtubules towards the plus end. Composed of two heavy (α) chains (110 kDa) and two or more light (β) chains (65-75 kDa). Also hydrolyses GTP.

References: [2659, 1050, 1764]

[EC 3.6.4.4 created 2000]

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EC 3.6.4.5

Accepted name: minus-end-directed kinesin ATPase

Reaction: ATP + H₂O = ADP + phosphate

Systematic name: kinesin ATP phosphohydrolase (minus-end-directed)

Comments: Structurally almost identical to EC 3.6.4.3 (microtubule-severing ATPase) but the movement it catalyses is towards the minus end of microtubules.

References: [984, 2294, 2171]

[EC 3.6.4.5 created 2000]

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EC 3.6.4.6

Accepted name: vesicle-fusing ATPase

Reaction: ATP + H₂O = ADP + phosphate

Systematic name: ATP phosphohydrolase (vesicle-fusing)

Comments: A large family of ATP-hydrolysing enzymes involved in the heterotopic fusion of membrane vesicles with target membranes and the homotypic fusion of various membrane compartments. They belong to the AAA-type (ATPase associated with a variety of cell activities) ATPase superfamily. They include peroxin, which apparently is involved in Zellweger’s syndrome.

References: [424, 1082, 97]

[EC 3.6.4.6 created 2000]
EC 3.6.4.7
Accepted name: peroxisome-assembly ATPase
Reaction: ATP + H$_2$O = ADP + phosphate
Other name(s): peroxisome assembly factor-2
Systematic name: ATP phosphohydrolase (peroxisome-assembling)
Comments: An extremely diversified group of enzymes that use the energy of ATP hydrolysis to import and assemble peroxisome components into the organelle. Their molecular masses range from 25 to 600 kDa.
References: [1413, 2610, 2840]

[EC 3.6.4.7 created 2000]

EC 3.6.4.8
Accepted name: proteasome ATPase
Reaction: ATP + H$_2$O = ADP + phosphate
Systematic name: ATP phosphohydrolase (polypeptide-degrading)
Comments: Belongs to the AAA-type superfamily and, like EC 3.6.4.5 (minus-end-directed kinesin ATPase), is involved in channel gating and polypeptide unfolding before proteolysis in the proteasome. Six ATPase subunits are present in the regulatory particle (RP) of 26S proteasome.
References: [2118, 1586]

[EC 3.6.4.8 created 2000]

EC 3.6.4.9
Accepted name: chaperonin ATPase
Reaction: ATP + H$_2$O = ADP + phosphate
Other name(s): chaperonin
Systematic name: ATP phosphohydrolase (polypeptide-unfolding)
Comments: Multisubunit proteins with 2x7 (Type I, in most cells) or 2x8 (Type II, in Archaea) ATP-binding sites involved in maintaining an unfolded polypeptide structure before folding or entry into mitochondria and chloroplasts. Molecular masses of subunits ranges from 10-90 kDa. They are a subclass of molecular chaperones that are related to EC 3.6.4.8 (proteasome ATPase).
References: [977, 1507, 2, 2058]

[EC 3.6.4.9 created 2000]

EC 3.6.4.10
Accepted name: non-chaperonin molecular chaperone ATPase
Reaction: ATP + H$_2$O = ADP + phosphate
Other name(s): molecular chaperone Hsc70 ATPase
Systematic name: ATP phosphohydrolase (polypeptide-polymerizing)
Comments: This is a highly diverse group of enzymes that perform many functions that are similar to those of chaperonins. They comprise a number of heat-shock-cognate proteins. They are also active in clathrin uncoating and in the oligomerization of actin.
References: [2174, 223, 2758, 2406, 1446]

[EC 3.6.4.10 created 2000]

EC 3.6.4.11
Accepted name: nucleoplasm ATPase
Reaction: ATP + H$_2$O = ADP + phosphate
Systematic name: ATP phosphohydrolase (nucleosome-assembling)
Comments: An acidic nuclear protein that is active in the ATP-dependent assembly of nucleosome cores, in decondensation of sperm chromatin and in other histone-involving processes.
EC 3.6.4.12
Accepted name: DNA helicase
Reaction: ATP + H₂O = ADP + phosphate
Other name(s): 3′ to 5′ DNA helicase; 5′-3′ DNA helicase; AvDH1; BACH1 helicase; BCmCM; BLM protein; BRCA1-associated C-terminal helicase; CeWRN-1; Dbp9p; Dm-RECQ5; DNA helicase 120; DNA helicase A; DNA helicase E; DNA helicase II; DNA helicase III; DNA helicase RECL5β; DNA helicase VI; dnaB; DNA helicase E1; helicase HDH IV; Hel E; helicase DnaB; helicase domain of bacteriophage T7 gene 4 protein helicase; PcrA helicase; UvrD; hHcsA; Hmi1p; hPif1; MCM helicase; MCM protein; MER3 helicase; MER3 protein; MPH1; PcrA; PcrA helicase; PDH120; PifDH A; Ph1p; PIF1
Systematic name: ATP phosphohydrolase (DNA helix unwinding)
Comments: DNA helicases utilize the energy from ATP hydrolysis to unwind double-stranded DNA. Some of them unwind duplex DNA with a 3′ to 5′ polarity [1,3,5,8], others show 5′ to 3′ polarity [10,11,12,13] or unwind DNA in both directions [1783, 2162]. Some helicases unwind DNA as well as RNA [729, 1108]. May be identical with EC 3.6.4.13 (RNA helicase).
References: [1924, 2525, 1763, 1394, 1971, 180, 1981, 466, 729, 1108, 1109, 2919, 795, 1783, 2162]

[EC 3.6.4.12 created 2009]

EC 3.6.4.13
Accepted name: RNA helicase
Reaction: ATP + H₂O = ADP + phosphate
Other name(s): CSFV NS3 helicase; DBP2; DbpA; DDX17; DDX25; DDX3; DDX3X; DDX3Y; DDX4; DDX5; DEAD-box protein DED1; DEAD-box RNA helicase; DEAH-box protein 2; DEAH-box RNA helicase; DED1; Dex(H/D) RNA helicase; EhDEAD1; EhDEAD1 RNA helicase; eIF4A helicase; KOKV helicase; Mtr4p; nonstructural protein 3 helicase; NPH-II; RHA; RNA helicase A; RNA helicase DDX3; RNA helicase Hera; RNA-dependent ATPase; TGBp1 NTPase/helicase domain; VRH1; GRTH/DDX25
Systematic name: ATP phosphohydrolase (RNA helix unwinding)
Comments: RNA helicases utilize the energy from ATP hydrolysis to unwind RNA. Some of them unwind RNA with a 3′ to 5′ polarity [1395], other show 5′ to 3′ polarity [?] . Some helicases unwind DNA as well as RNA [729, ?]. May be identical with EC 3.6.4.12 (DNA helicase).
References: [438, 2132, 1395, 1444, 2828, 880, 729, ?]

[EC 3.6.4.13 created 2009]

EC 3.6.5 Acting on GTP to facilitate cellular and subcellular movement

EC 3.6.5.1
Accepted name: heterotrimeric G-protein GTPase
Reaction: GTP + H₂O = GDP + phosphate
Systematic name: GTP phosphohydrolase (signalling)
Comments: This group comprises GTP-hydrolysing systems, where GTP and GDP alternate in binding. This group includes stimulatory and inhibitory G-proteins such as Gₐ, Gᵢ, Gᵣ, and Gₒ₁f, targeting adenylate cyclase and/or K⁺ and Ca²⁺ channels; Gq stimulating phospholipase C; transducin activating cGMP phosphodiesterase; gustducin activating cAMP phosphodiesterase. Gₒ₁f is instrumental in odour perception, transducin in vision and gustducin in taste recognition. At least 16 different α subunits (39-52 kDa), 5 β subunits (36 kDa) and 12 γ subunits (6-9 kDa) are known.
References: [1791, 2402, 239, 1670]
EC 3.6.5.2

**Accepted name:** small monomeric GTPase  
**Reaction:** GTP + H₂O = GDP + phosphate  
**Systematic name:** GTP phosphohydrolase (cell-regulating)  
**Comments:** A family of about 50 enzymes with a molecular mass of 21 kDa that are distantly related to the α-subunit of heterotrimeric G-protein GTPase (EC 3.6.5.1). They are involved in cell-growth regulation (Ras subfamily), membrane vesicle traffic and uncoating (Rab and ARF subfamilies), nuclear protein import (Ran subfamily) and organization of the cytoskeleton (Rho and Rac subfamilies).  
**References:** [247, 908, 800, 2698]

EC 3.6.5.3

**Accepted name:** protein-synthesizing GTPase  
**Reaction:** GTP + H₂O = GDP + phosphate  
**Other name(s):** elongation factor (EF); initiation factor (IF); peptide-release or termination factor  
**Systematic name:** GTP phosphohydrolase (mRNA-translation-assisting)  
**Comments:** This enzyme comprises a family of proteins involved in prokaryotic as well as eukaryotic protein synthesis. In the initiation factor complex, it is IF-2b (98 kDa) that binds GTP and subsequently hydrolyses it in prokaryotes. In eukaryotes, it is eIF-2 (150 kDa) that binds GTP. In the elongation phase, the GTP-hydrolysing proteins are the EF-Tu polypeptide of the prokaryotic transfer factor (43 kDa), the eukaryotic elongation factor EF-1α (53 kDa), the prokaryotic EF-G (77 kDa), the eukaryotic EF-2 (70-110 kDa) and the signal recognition particle that play a role in endoplasmic reticulum protein synthesis (325 kDa). EF-Tu and EF-1α catalyse binding of aminoacyl-tRNA to the ribosomal A-site, while EF-G and EF-2 catalyse the translocation of peptidyl-tRNA from the A-site to the P-site. GTPase activity is also involved in polypeptide release from the ribosome with the aid of the pRFs and eRFs.  
**References:** [1365, 1276, 2134, 721, 1321]

EC 3.6.5.4

**Accepted name:** signal-recognition-particle GTPase  
**Reaction:** GTP + H₂O = GDP + phosphate  
**Systematic name:** GTP phosphohydrolase (protein-synthesis-assisting)  
**Comments:** Activity is associated with the signal-recognition particle (a protein- and RNA-containing structure involved in endoplasmic-reticulum-associated protein synthesis).  
**References:** [430, 431, 1659, 728]

EC 3.6.5.5

**Accepted name:** dynamin GTPase  
**Reaction:** GTP + H₂O = GDP + phosphate  
**Systematic name:** GTP phosphohydrolase (vesicle-releasing)  
**Comments:** An enzyme with a molecular mass of about 100 kDa that is involved in endocytosis and is instrumental in pinching off membrane vesicles.  
**References:** [2748, 1612, 1871]
EC 3.6.5.6

Accepted name: tubulin GTPase
Reaction: GTP + H₂O = GDP + phosphate
Systematic name: GTP phosphohydrolase (microtubule-releasing)
Comments: An intrinsic activity of α-tubulin involved in tubulin folding, division plane formation in prokaryotic cells and others.
References: [2899, 2562, 2159]

[EC 3.6.5.6 created 2000 as EC 3.6.1.51, transferred 2003 to EC 3.6.5.6]

EC 3.7 Acting on carbon-carbon bonds

This subclass contains a single sub-subclass for those enzymes that act on carbon-carbon bonds in ketonic substances (EC 3.7.1). There are relatively few carbon-carbon hydrolases and they mostly catalyse the hydrolysis of 3-oxo-carboxylic acids.

EC 3.7.1 In ketonic substances

EC 3.7.1.1

Accepted name: oxaloacetase
Reaction: oxaloacetate + H₂O = oxalate + acetate
Other name(s): oxalacetic hydrolase
Systematic name: oxaloacetate acetylhydrolase
References: [959]

[EC 3.7.1.1 created 1961]

EC 3.7.1.2

Accepted name: fumarylacetoacetase
Reaction: 4-fumarylacetoacetate + H₂O = acetoacetate + fumarate
Other name(s): β-diketonase; fumarylacetoacetate hydrolase
Systematic name: 4-fumarylacetoacetate fumarylhydrolase
Comments: Also acts on other 3,5- and 2,4-dioxo acids.
References: [433, 607, 1631]

[EC 3.7.1.2 created 1961]

EC 3.7.1.3

Accepted name: kynureninase
Reaction: L-kynurenine + H₂O = anthranilate + L-alanine
Systematic name: L-kynurenine hydrolase
Comments: A pyridoxal-phosphate protein. Also acts on 3′-hydroxy-L-kynurenine and some other (3-arylcarbonyl)-alanines.
References: [1126, 1125, 1287, 2814]

[EC 3.7.1.3 created 1965]

EC 3.7.1.4

Accepted name: phloretin hydrolase
Reaction: phloretin + H₂O = phloretate + phloroglucinol
Other name(s): lactase-phlorizin hydrolase
Systematic name: 2′,4,4′,6′-tetrahydroxydehydrochalcone 1,3,5-trihydroxybenzenehydrolase
Comments: Also hydrolyses other C-acylated phenols related to phloretin.
References: [1669]

[EC 3.7.1.4 created 1972]

EC 3.7.1.5
Accepted name: acylpyruvate hydrolase
Reaction: a 3-acylpyruvate + H₂O = a carboxylate + pyruvate
Systematic name: 3-acylpyruvate acylhydrolase
Comments: Acts on formylpyruvate, 2,4-dioxopentanoate, 2,4-dioxohexanoate and 2,4-dioxoheptanoate.
References: [2755]

[EC 3.7.1.5 created 1976]

EC 3.7.1.6
Accepted name: acetylpyruvate hydrolase
Reaction: acetylpyruvate + H₂O = acetate + pyruvate
Systematic name: 2,4-dioxopentanoate acetylhydrolase
Comments: Highly specific; does not act on pyruvate, oxaloacetate, maleylpyruvate, fumarylpyruvate or acetylacetone.
References: [482]

[EC 3.7.1.6 created 1984]

EC 3.7.1.7
Accepted name: β-diketone hydrolase
Reaction: nonane-4,6-dione + H₂O = pentan-2-one + butanoate
Other name(s): oxidized PVA hydrolase
Systematic name: nonane-4,6-dione acylhydrolase
Comments: Also acts on the product of the action of EC 1.1.3.18 secondary-alcohol oxidase, on polyvinyl alcohols; involved in the bacterial degradation of polyvinyl alcohol.
References: [2186, 2187]

[EC 3.7.1.7 created 1989]

EC 3.7.1.8
Accepted name: 2,6-dioxo-6-phenylhexa-3-enoate hydrolase
Reaction: 2,6-dioxo-6-phenylhexa-3-enoate + H₂O = benzoate + 2-oxopent-4-enoate
Other name(s): HOHPDA hydrolase
Systematic name: 2,6-dioxo-6-phenylhexa-3-enoate benzylyhydrolase
Comments: Cleaves the products from biphenol, 3-isopropylcatechol and 3-methylcatechol produced by EC 1.13.11.39 biphenyl-2,3-diol 1,2-dioxygenase, by ring-fission at a -CO-C bond. Involved in the breakdown of biphenyl-related compounds by Pseudomonas sp.
References: [1903]

[EC 3.7.1.8 created 1989]

EC 3.7.1.9
Accepted name: 2-hydroxymuconate-semialdehyde hydrolase
Reaction: 2-hydroxymuconate semialdehyde + H₂O = formate + 2-oxopent-4-enoate
Other name(s): 2-hydroxy-6-oxohepta-2,4-dienoate hydrolase; 2-hydroxymuconic semialdehyde hydrolase; HMSH; HOD hydrolase

[EC 3.7.1.9 created 1989]
Systematic name: 2-hydroxymuconate-semialdehyde formylhydrolase

References: [925, 2191]

[EC 3.7.1.9 created 1990]

EC 3.7.1.10
Accepted name: cyclohexane-1,3-dione hydrolase
Reaction: cyclohexane-1,3-dione + H₂O = 5-oxohexanoate
Other name(s): 1,3-cyclohexanedione hydrolase
Systematic name: cyclohexane-1,3-dione acylhydrolase (decyclizing)
Comments: Highly specific; does not act on other dione derivatives of cyclohexane, cyclopentane or cycloheptane.
References: [475]

[EC 3.7.1.10 created 1992]

EC 3.7.1.11
Accepted name: cyclohexane-1,2-dione hydrolase
Reaction: cyclohexane-1,2-dione + H₂O = 6-oxohexanoate
Systematic name: cyclohexane-1,2-dione acylhydrolase (decyclizing)
Comments: Highly specific; does not act on cyclohexanone or cyclohexane-1,3-dione as substrate.
References: [926, 717]

[EC 3.7.1.11 created 2009]

EC 3.8 Actating on halide bonds
This subclass contains enzymes that hydrolyse carbon-halide compounds in a single sub-subclass (EC 3.8.1).

EC 3.8.1 In carbon-halide compounds

EC 3.8.1.1
Accepted name: alkylhalidase
Reaction: bromochloromethane + H₂O = formaldehyde + bromide + chloride
Other name(s): halogenase; haloalkane halidohydrolase; haloalkane dehalogenase
Systematic name: alkyl-halide halidohydrolase
References: [992]

[EC 3.8.1.1 created 1961]

EC 3.8.1.2
Accepted name: (S)-2-haloacid dehalogenase
Reaction: (S)-2-haloacid + H₂O = (R)-2-hydroxyacid + halide
Other name(s): 2-haloacid dehalogenase[ambiguous]; 2-haloacid halidohydrolase [ambiguous][ambiguous]; 2-haloalkanoic acid dehalogenase; 2-haloalkanoid acid halidohydrolase; 2-halocarboxylic acid dehalogenase II; DL-2-haloacid dehalogenase[ambiguous]; L-2-haloacid dehalogenase; l-DEX
Systematic name: (S)-2-haloacid halidohydrolase
Comments: Acts on acids of short chain lengths, C₂ to C₄, with inversion of configuration at C-2. [See also EC 3.8.1.9 (R)-2-haloacid dehalogenase, EC 3.8.1.10 2-haloacid dehalogenase (configuration-inverting) and EC 3.8.1.11 2-haloacid dehalogenase (configuration-retaining)]
References: [843, 1724, 1278, 542, 1717, 1296, 1721, 1357, 2376]
EC 3.8.1.3  
Accepted name: haloacetate dehalogenase  
Reaction: haloacetate + H₂O = glycolate + halide  
Other name(s): monohaloacetate dehalogenase  
Systematic name: haloacetate halidohydrolase  
References: [840, 842]

[EC 3.8.1.3 created 1972]

EC 3.8.1.5  
Accepted name: haloalkane dehalogenase  
Reaction: 1-haloalkane + H₂O = a primary alcohol + halide  
Other name(s): 1-chlorohexane halidohydrolase; 1-haloalkane dehalogenase  
Systematic name: 1-haloalkane halidohydrolase  
Comments: Acts on a wide range of 1-haloalkanes, haloalcohols, haloalkenes and some haloaromatic compounds.  
References: [1243, 2255, 2884]

[EC 3.8.1.5 created 1989]

EC 3.8.1.6  
Accepted name: 4-chlorobenzoate dehalogenase  
Reaction: 4-chlorobenzoate + H₂O = 4-hydroxybenzoate + chloride  
Other name(s): halobenzoate dehalogenase  
Systematic name: 4-chlorobenzoate chlorohydrolase  
Comments: Catalyses the first step in the degradation of chlorobenzoate in Pseudomonas. In many microorganisms, this activity comprises three separate enzymes, EC 6.2.1.33 (4-chlorobenzoate—CoA ligase), EC 3.8.1.7 (4-chlorobenzoyl-CoA dehalogenase) and EC 3.1.2.23 (4-hydroxybenzoyl-CoA thioesterase).  
References: [1731, 992]

[EC 3.8.1.6 created 1989, modified 1999]

EC 3.8.1.7  
Accepted name: 4-chlorobenzoyl-CoA dehalogenase  
Reaction: 4-chlorobenzoyl-CoA + H₂O = 4-hydroxybenzoyl CoA + chloride  
Systematic name: 4-chlorobenzoyl CoA chlorohydrolase  
Comments: Specific for dehalogenation at the 4-position. Can dehalogenate substrates bearing fluorine, chlorine, bromine and iodine in the 4-position. This enzyme is part of the bacterial 2,4-dichlorobenzoate degradation pathway.  
References: [359, 456]

[EC 3.8.1.7 created 1999]

EC 3.8.1.8  
Accepted name: atrazine chlorohydrolase  
Reaction: atrazine + H₂O = 4-(ethylamino)-2-hydroxy-6-(isopropylamino)-1,3,5-triazine + HCl  
Other name(s): AtzA

[EC 3.8.1.8 created 1999]
atrazine chlorohydrolase

Involved in the degradation of the herbicide atrazine, 2-chloro-4-(ethylamino)-6-(isopropylamino)-1,3,5-triazine, in bacteria.

[502, 501]

[EC 3.8.1.8 created 2000]

EC 3.8.1.9

Accepted name: (R)-2-haloacid dehalogenase

Reaction: (R)-2-haloacid + H₂O = (S)-2-hydroxyacid + halide

Other name(s): 2-haloalkanoic acid dehalogenase[ambiguous]; 2-haloalkanoid acid halidohydrolase[ambiguous]; D-2-haloacid dehalogenase; D-DEX

Systematic name: (R)-2-haloacid halidohydrolase

Comments: Acts on acids of short chain lengths, C₂ to C₄, with inversion of configuration at C-2. [See also EC 3.8.1.2 (S)-2-haloacid dehalogenase, EC 3.8.1.10 2-haloacid dehalogenase (configuration-inverting) and EC 3.8.1.11 2-haloacid dehalogenase (configuration-retaining)]

References: [2366, 1416, 2376]

[EC 3.8.1.9 created 2003]

EC 3.8.1.10

Accepted name: 2-haloacid dehalogenase (configuration-inverting)

Reaction: (1) (S)-2-haloacid + H₂O = (R)-2-hydroxyacid + halide
(2) (R)-2-haloacid + H₂O = (S)-2-hydroxyacid + halide

Other name(s): 2-haloalkanoic acid dehalogenase; 2-haloalkanoid acid halidohydrolase; DL-2-haloacid dehalogenase; DL-2-haloacid halidohydrolase (inversion of configuration); DL-DEX; (R,S)-2-haloacid dehalogenase (configuration-inverting)

Systematic name: (S)-2-haloacid dehalogenase (configuration-inverting)

Comments: Dehalogenates both (S)- and (R)-2-haloalkanoic acids to the corresponding (R)- and (S)-2-hydroxyalkanoic acids, respectively, with inversion of configuration at C-2. The enzyme from Pseudomonas sp. 113 acts on 2-haloalkanoic acids whose carbon chain lengths are five or less. [See also EC 3.8.1.2 (S)-2-haloacid dehalogenase, EC 3.8.1.9 (R)-2-haloacid dehalogenase and EC 3.8.1.11 2-haloacid dehalogenase (configuration-retaining)]

References: [1721, 1723, 1722, 1357, 1485, 324, 1416, 2768, 2376]

[EC 3.8.1.10 created 2003]

EC 3.8.1.11

Accepted name: 2-haloacid dehalogenase (configuration-retaining)

Reaction: (1) (S)-2-haloacid + H₂O = (S)-2-hydroxyacid + halide
(2) (R)-2-haloacid + H₂O = (R)-2-hydroxyacid + halide

Other name(s): 2-haloalkanoic acid dehalogenase; 2-haloalkanoid acid halidohydrolase; DL-2-haloacid dehalogenase; DL-DEXr

Systematic name: (S)-2-haloacid dehalogenase (configuration-retaining)

Comments: Dehalogenates both (S)- and (R)-2-haloalkanoic acids to the corresponding (S)- and (R)-2-hydroxyalkanoic acids, respectively, with retention of configuration at C-2. [See also EC 3.8.1.2 (S)-2-haloacid dehalogenase, EC 3.8.1.9 (R)-2-haloacid dehalogenase and EC 3.8.1.10 2-haloacid dehalogenase (configuration-inverting)]

References: [2768, 2376]

[EC 3.8.1.11 created 2003]
EC 3.8.2 In phosphorus-halide compounds (deleted sub-subclass)


[EC 3.8.2.1 created 1961, modified 1976, deleted 1992]

EC 3.9 Acting on phosphorus-nitrogen bonds

This subclass contains a single sub-subclass for enzymes that act on phosphorus-nitrogen bonds (EC 3.9.1).

EC 3.9.1 Acting on phosphorus-nitrogen bonds (only sub-subclass identified to date)

EC 3.9.1.1

Accepted name: phosphoamidase
Reaction: \( N\text{-phosphocreatine} + H_2O = \text{creatine} + \text{phosphate} \)
Other name(s): creatine phosphatase
Systematic name: phosphamide hydrolase
Comments: Also acts on \( N\text{-phospho-arginine} \) and other phosphoamides. Possibly identical with EC 3.1.3.9 (glucose-6-phosphatase) or EC 3.1.3.16 (phosphoprotein phosphatase).
References: [1942, 2335, 2450]

[EC 3.9.1.1 created 1961]

EC 3.10 Acting on sulfur-nitrogen bonds

This subclass contains a single sub-subclass for enzymes that act on sulfur-nitrogen bonds (EC 3.10.1).

EC 3.10.1 Acting on sulfur-nitrogen bonds (only sub-subclass identified to date)

EC 3.10.1.1

Accepted name: \( N\text{-sulfo-D-glucosamine sulfohydrolase} \)
Reaction: \( N\text{-sulfo-D-glucosamine} + H_2O = \text{D-glucosamine} + \text{sulfate} \)
Other name(s): sulfogluosamine sulfamidase; heparin sulfamidase; 2-desoxy-D-glucoside-2-sulphamate sulfohydrolase (sulphamate sulfohydrolase)
Systematic name: \( N\text{-sulfo-D-glucosamine sulfohydrolase} \)
References: [541, 1532]

[EC 3.10.1.1 created 1972, modified 1981, modified 1982]

EC 3.10.1.2

Accepted name: cyclamate sulfohydrolase
Reaction: \( \text{cyclohexylsulfamate} + H_2O = \text{cyclohexylamine} + \text{sulfate} \)
Other name(s): cyclamate sulfamidase; cyclamate sulfamidase; cyclohexylsulfamate sulfamidase
Systematic name: cyclohexylsulfamate sulfohydrolase
Comments: Also readily hydrolyses aliphatic sulfamates with 3 to 8 carbons.
References: [1806]

[EC 3.10.1.2 created 1976, modified 1981]
**EC 3.11 Acting on carbon-phosphorus bonds**

This subclass contains a single sub-subclass for enzymes that hydrolyse C-phosphono-groups (EC 3.11.1).

**EC 3.11.1 Acting on carbon-phosphorus bonds (only sub-subclass identified to date)**

**EC 3.11.1.1**

**Accepted name:** phosphonoacetaldehyde hydrolase  
**Reaction:** phosphonoacetaldehyde + H₂O = acetaldehyde + phosphate  
**Other name(s):** phosphonatase; 2-phosphonoacetylaldehyde phosphonohydrolase  
**Systematic name:** 2-oxoethylphosphonate phosphonohydrolase  
**Comments:** This enzyme destabilizes the C-P bond, by forming an imine between one of its lysine residues and the carbonyl group of the substrate, thus allowing this, normally stable, bond to be broken. The mechanism is similar to that used by EC 4.1.2.13, fructose-bisphosphate aldolase, to break a C-C bond. Belongs to the haloacetate dehalogenase family.  
**References:** [1787, 1788, 1786, 1899, 109]

[EC 3.11.1.1 created 1972, modified 1976, modified 2001]

**EC 3.11.1.2**

**Accepted name:** phosphonoacetate hydrolase  
**Reaction:** phosphonoacetate + H₂O = acetate + phosphate  
**Systematic name:** phosphonoacetate phosphonohydrolase  
**Comments:** A zinc-dependent enzyme. Belongs to the alkaline phosphatase superfamily of zinc-dependent hydrolases.  
**References:** [1620]

[EC 3.11.1.2 created 1999]

**EC 3.11.1.3**

**Accepted name:** phosphonopyruvate hydrolase  
**Reaction:** 3-phosphonopyruvate + H₂O = pyruvate + phosphate  
**Other name(s):** PPH  
**Comments:** Highly specific for phosphonopyruvate as substrate [1340]. The reaction is not inhibited by phosphate but is inhibited by the phosphonates phosphonoformic acid, hydroxymethylphosphonic acid and 3-phophonopropanoic acid [1340]. The enzyme is activated by the divalent cations Co²⁺, Mg²⁺ and Mn²⁺. This enzyme is a member of the phosphoenolpyruvate mutase/isocitrate lyase superfamily [373].  
**References:** [2544, 1340, 373]

[EC 3.11.1.3 created 2007]

**EC 3.12 Acting on sulfur-sulfur bonds**

This subclass contains a single sub-subclass for enzymes that act on sulfur-sulfur bonds (EC 3.12.1).

**EC 3.12.1 Acting on sulfur-sulfur bonds (only sub-subclass identified to date)**

**EC 3.12.1.1**
Accepted name: trithionate hydrolase
Reaction: trithionate + H₂O = thiosulfate + sulfate + 2 H⁺
Systematic name: trithionate thiosulfohydrolase
References: [1504, 2597]

[EC 3.12.1.1 created 1990]

**EC 3.13 Acting on carbon-sulfur bonds**

This subclass contains a single sub-subclass for enzymes that act on carbon-sulfur bonds (EC 3.13.1).

**EC 3.13.1 Acting on carbon-sulfur bonds (only sub-subclass identified to date)**

**EC 3.13.1.1**

Accepted name: UDP-sulfoquinovose synthase
Reaction: UDP-glucose + sulfite = UDP-6-sulfoquinovose + H₂O
Other name(s): sulfite:UDP-glucose sulfotransferase; UDPsulfoquinovose synthase
Systematic name: UDP-6-sulfo-6-deoxyglucose sulfohydrolase
Comments: Requires NAD⁺, which appears to oxidize the substrate to UDP-4-dehydroglucose, which dehydrates to UDP-4-dehydro-6-deoxygluc-5-enose, to which sulfite can add; the reaction is completed when the substrate is rehydrogenated at C-4. The enzyme from *Arabidopsis thaliana* is specific for UDP-Glc and sulfite.
References: [644, 645, 1727, 2197]

[EC 3.13.1.1 created 2001]

[3.13.1.2 Deletes entry. 5-deoxyribose-5-ylhomocysteinase. The activity is most probably attributable to EC 4.4.1.21, S-ribosylhomocysteine lyase]

[EC 3.13.1.2 created 1972 as EC 3.3.1.3, transferred 2001 to EC 3.2.1.148, transferred 2004 to EC 3.13.1.2, deleted 2005]

**EC 3.13.1.3**

Accepted name: 2′-hydroxybiphenyl-2-sulfinate desulfinase
Reaction: 2′-hydroxybiphenyl-2-sulfinate + H₂O = 2-hydroxybiphenyl + sulfite
Other name(s): gene dszB-encoded hydrolase; 2-(2-hydroxyphenyl) benzenesulfinate:H₂O hydrolase; DszB; HBPSi desulfinase; 2-(2-hydroxyphenyl) benzenesulfinate sulfohydrolase; HPBS desulfinase; 2-(2-hydroxyphenyl) benzenesulfinate hydrolase; 2-(2′-hydroxyphenyl) benzenesulfinate desulfinase; 2-(2-hydroxyphenyl) benzenesulfinate desulfinase
Systematic name: 2′-hydroxybiphenyl-2-sulfinate sulfohydrolase
Comments: The enzyme from *Rhodococcus* sp. strain IGTS8 is encoded by the plasmid-encoded dibenzothiophene-desulfurization (dsz) operon. The enzyme has a narrow substrate specificity with biphenyl-2-sulfinate being the only other substrate known to date [1779].
References: [1898, 1779, 2754]

[EC 3.13.1.3 created 2000 as EC 3.1.2.24, transferred 2005 to EC 3.13.1.3]
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