

The Enzyme List

Class 7 — Translocases

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

L^AT_EX version prepared by Andrew McDonald,
School of Biochemistry and Immunology, Trinity College Dublin, Ireland

Generated from the [ExplorEnz](#) database, May 2023

© 2023 IUBMB

Contents

EC 7.1 Catalysing the translocation of hydrons	1
EC 7.1.1 Linked to oxidoreductase reactions	1
EC 7.1.2 Linked to the hydrolysis of a nucleoside triphosphate	5
EC 7.1.3 Linked to the hydrolysis of diphosphate	6
EC 7.2 Catalysing the translocation of inorganic cations	7
EC 7.2.1 Linked to oxidoreductase reactions	7
EC 7.2.2 Linked to the hydrolysis of a nucleoside triphosphate	7
EC 7.2.3 Linked to the hydrolysis of a nucleoside triphosphate	13
EC 7.2.4 Linked to decarboxylation	13
EC 7.3 Catalysing the translocation of inorganic anions and their chelates	15
EC 7.3.2 Linked to the hydrolysis of a nucleoside triphosphate	15
EC 7.4 Catalysing the translocation of amino acids and peptides	17
EC 7.4.2 Linked to the hydrolysis of a nucleoside triphosphate	18
EC 7.5 Catalysing the translocation of carbohydrates and their derivatives	21
EC 7.5.2 Linked to the hydrolysis of a nucleoside triphosphate	22
EC 7.6 Catalysing the translocation of other compounds	25
EC 7.6.2 Linked to the hydrolysis of a nucleoside triphosphate	25
References	31
Index	46

EC 7.1 Catalysing the translocation of hydrons

EC 7.1.1 Linked to oxidoreductase reactions

EC 7.1.1.1

- Accepted name:** proton-translocating NAD(P)⁺ transhydrogenase
Reaction: $\text{NADPH} + \text{NAD}^+ + \text{H}^+_{[\text{side 1}]} = \text{NADP}^+ + \text{NADH} + \text{H}^+_{[\text{side 2}]}$
Other name(s): *pntA* (gene name); *pntB* (gene name); NNT (gene name)
Systematic name: NADPH:NAD⁺ oxidoreductase (H⁺-transporting)
Comments: The enzyme is a membrane bound proton-translocating pyridine nucleotide transhydrogenase that couples the reversible reduction of NADP by NADH to an inward proton translocation across the membrane. In the bacterium *Escherichia coli* the enzyme provides a major source of cytosolic NADPH. Detoxification of reactive oxygen species in mitochondria by glutathione peroxidases depends on NADPH produced by this enzyme.
References: [56, 57, 82, 216, 35, 272, 116, 167]

[EC 7.1.1.1 created 2015 as EC 1.6.1.5, transferred 2018 to EC 7.1.1.1]

EC 7.1.1.2

- Accepted name:** NADH:ubiquinone reductase (H⁺-translocating)
Reaction: $\text{NADH} + \text{ubiquinone} + 6 \text{H}^+_{[\text{side 1}]} = \text{NAD}^+ + \text{ubiquinol} + 7 \text{H}^+_{[\text{side 2}]}$
Other name(s): ubiquinone reductase (ambiguous); type 1 dehydrogenase; complex I dehydrogenase; coenzyme Q reductase (ambiguous); complex I (electron transport chain); complex I (mitochondrial electron transport); complex I (NADH:Q1 oxidoreductase); dihydronicotinamide adenine dinucleotide-coenzyme Q reductase (ambiguous); DPNH-coenzyme Q reductase (ambiguous); DPNH-ubiquinone reductase (ambiguous); mitochondrial electron transport complex 1; mitochondrial electron transport complex I; NADH coenzyme Q₁ reductase; NADH-coenzyme Q oxidoreductase (ambiguous); NADH-coenzyme Q reductase (ambiguous); NADH-CoQ oxidoreductase (ambiguous); NADH-dehydrogenase (ubiquinone) (ambiguous); NADH-CoQ reductase (ambiguous); NADH-ubiquinone reductase (ambiguous); NADH-ubiquinone oxidoreductase (ambiguous); NADH-ubiquinone-1 reductase; reduced nicotinamide adenine dinucleotide-coenzyme Q reductase (ambiguous); NADH:ubiquinone oxidoreductase complex; NADH-Q6 oxidoreductase (ambiguous); electron transfer complex I; NADH₂ dehydrogenase (ubiquinone)
Systematic name: NADH:ubiquinone oxidoreductase
Comments: The enzyme is a very large complex that participates in electron transfer chains of mitochondria and aerobic bacteria, transferring electrons from NADH to the ubiquinone pool. Reversed electron transport through this enzyme can reduce NAD⁺ to NADH.
References: [91, 96, 109, 70, 274]

[EC 7.1.1.2 created 1961 as EC 1.6.5.3, deleted 1965, reinstated 1983, modified 2011, modified 2013, transferred 2018 to EC 7.1.1.2]

EC 7.1.1.3

- Accepted name:** ubiquinol oxidase (H⁺-transporting)
Reaction: $2 \text{ubiquinol} + \text{O}_2 + n \text{H}^+_{[\text{side 1}]} = 2 \text{ubiquinone} + 2 \text{H}_2\text{O} + n \text{H}^+_{[\text{side 2}]}$
Other name(s): cyoABCD (gene names); cytochrome *bo*₃ oxidase; cytochrome *bb*₃ oxidase; cytochrome *bo* oxidase; ubiquinol:O₂ oxidoreductase (H⁺-transporting)
Systematic name: ubiquinol:oxygen oxidoreductase (H⁺-transporting)
Comments: Contains a dinuclear centre comprising two hemes, or heme and copper. This terminal oxidase enzyme generates proton motive force by two mechanisms: (1) transmembrane charge separation resulting from utilizing protons and electrons originating from opposite sides of the membrane to generate water, and (2) active pumping of protons across the membrane. The bioenergetic efficiency (the number of charges driven across the membrane per electron used to reduce oxygen to water) depends on the enzyme; for example, for the *bo*₃ oxidase it is 2. *cf.* EC 7.1.1.7, ubiquinol oxidase ubiquinol oxidase (electrogenic, proton-motive force generating).
References: [3, 243, 280, 54, 55]

[EC 7.1.1.3 created 2011 as EC 1.10.3.10, modified 2014, transferred 2018 to EC 7.1.1.3]

EC 7.1.1.4

- Accepted name:** caldariellaquinol oxidase (H⁺-transporting)
- Reaction:** $2 \text{ caldariellaquinol} + \text{O}_2 + n \text{ H}^+_{[\text{side 1}]} = 2 \text{ caldariellaquinone} + 2 \text{ H}_2\text{O} + n \text{ H}^+_{[\text{side 2}]}$
- Other name(s):** SoxABCD quinol oxidase; SoxABCD complex; quinol oxidase SoxABCD; SoxM supercomplex; *aa*₃-type quinol oxidase; *aa*₃ quinol oxidase; cytochrome *aa*₃; terminal quinol oxidase; terminal quinol:oxygen oxidoreductase; caldariella quinol:dioxygen oxidoreductase; cytochrome *aa*₃-type oxidase; caldariellaquinol:O₂ oxidoreductase (H⁺-transporting)
- Systematic name:** caldariellaquinol:oxygen oxidoreductase (H⁺-transporting)
- Comments:** A copper-containing cytochrome. The enzyme from thermophilic archaea is part of the terminal oxidase and catalyses the reduction of O₂ to water, accompanied by the extrusion of protons across the cytoplasmic membrane.
- References:** [83, 199, 80, 131, 176, 13]

[EC 7.1.1.4 created 2013 as EC 1.10.3.13, transferred 2018 to EC 7.1.1.4]

EC 7.1.1.5

- Accepted name:** menaquinol oxidase (H⁺-transporting)
- Reaction:** $2 \text{ menaquinol} + \text{O}_2 + n \text{ H}^+_{[\text{side 1}]} = 2 \text{ menaquinone} + 2 \text{ H}_2\text{O} + n \text{ H}^+_{[\text{side 2}]}$
- Other name(s):** cytochrome *aa*₃-600 oxidase; cytochrome *bd* oxidase; menaquinol:O₂ oxidoreductase (H⁺-transporting)
- Systematic name:** menaquinol:oxygen oxidoreductase (H⁺-transporting)
- Comments:** Cytochrome *aa*₃-600, one of the principal respiratory oxidases from *Bacillus subtilis*, is a member of the heme-copper superfamily of oxygen reductases, and is a close homologue of the cytochrome *bo*₃ ubiquinol oxidase from *Escherichia coli*, but uses menaquinol instead of ubiquinol as a substrate. The enzyme also pumps protons across the membrane bilayer, generating a proton motive force.
- References:** [138, 141, 281]

[EC 7.1.1.5 created 2011 as EC 1.10.3.12, transferred 2018 to EC 7.1.1.5]

EC 7.1.1.6

- Accepted name:** plastoquinol—plastocyanin reductase
- Reaction:** $\text{plastoquinol} + 2 \text{ oxidized plastocyanin} + 2 \text{ H}^+_{[\text{side 1}]} = \text{plastoquinone} + 2 \text{ reduced plastocyanin} + 4 \text{ H}^+_{[\text{side 2}]}$
- Other name(s):** plastoquinol/plastocyanin oxidoreductase; cytochrome *f/b*₆ complex; cytochrome *b*₆*f* complex
- Systematic name:** plastoquinol:oxidized-plastocyanin oxidoreductase
- Comments:** Contains two *b*-type cytochromes, two *c*-type cytochromes (*c*_n and *f*), and a [2Fe-2S] Rieske cluster. The enzyme plays a key role in photosynthesis, transferring electrons from photosystem II (EC 1.10.3.9) to photosystem I (EC 1.97.1.12). Cytochrome *c*-552 can act as acceptor instead of plastocyanin, but more slowly. In chloroplasts, protons are translocated through the thylakoid membrane from the stroma to the lumen. The mechanism occurs through the Q cycle as in EC 7.1.1.8, quinol—cytochrome-*c* reductase (complex III) and involves electron bifurcation.
- References:** [110, 62]

[EC 7.1.1.6 created 1984 as EC 1.10.99.1, transferred 2011 to EC 1.10.9.1, transferred 2018 to EC 7.1.1.6]

EC 7.1.1.7

- Accepted name:** quinol oxidase (electrogenic, proton-motive force generating)
- Reaction:** $2 \text{ quinol} + \text{O}_2_{[\text{side 2}]} + 4 \text{ H}^+_{[\text{side 2}]} = 2 \text{ quinone} + 2 \text{ H}_2\text{O}_{[\text{side 2}]} + 4 \text{ H}^+_{[\text{side 1}]}$ (overall reaction)
(1a) $2 \text{ quinol} = 2 \text{ quinone} + 4 \text{ H}^+_{[\text{side 1}]} + 4 \text{ e}^-$
(1b) $\text{O}_2_{[\text{side 2}]} + 4 \text{ H}^+_{[\text{side 2}]} + 4 \text{ e}^- = 2 \text{ H}_2\text{O}_{[\text{side 2}]}$

Other name(s): *cydAB* (gene names); *appBC* (gene names); cytochrome *bd* oxidase; cytochrome *bd*-I oxidase; cytochrome *bd*-II oxidase; ubiquinol:O₂ oxidoreductase (electrogenic, non H⁺-transporting); ubiquinol oxidase (electrogenic, proton-motive force generating); ubiquinol oxidase (electrogenic, non H⁺-transporting)

Systematic name: quinol:oxygen oxidoreductase (electrogenic, non H⁺-transporting)

Comments: This terminal oxidase enzyme is unable to pump protons but generates a proton motive force by transmembrane charge separation resulting from utilizing protons and electrons originating from opposite sides of the membrane to generate water. The bioenergetic efficiency (the number of charges driven across the membrane per electron used to reduce oxygen to water) is 1. The *bd*-I oxidase from the bacterium *Escherichia coli* is the predominant respiratory oxygen reductase that functions under microaerophilic conditions in that organism. *cf.* EC 7.1.1.3, ubiquinol oxidase (H⁺-transporting).

References: [171, 200, 21, 142, 226, 40, 39]

[EC 7.1.1.7 created 2014 as EC 1.10.3.14, modified 2017, transferred 2018 to EC 7.1.1.7, modified 2020]

EC 7.1.1.8

Accepted name: quinol—cytochrome-*c* reductase

Reaction: quinol + 2 ferricytochrome *c* = quinone + 2 ferrocycytochrome *c* + 2 H⁺_[side 2]

Other name(s): ubiquinol—cytochrome-*c* reductase; coenzyme Q-cytochrome *c* reductase; dihydrocoenzyme Q-cytochrome *c* reductase; reduced ubiquinone-cytochrome *c* reductase; complex III (mitochondrial electron transport); ubiquinone-cytochrome *c* reductase; ubiquinol-cytochrome *c* oxidoreductase; reduced coenzyme Q-cytochrome *c* reductase; ubiquinone-cytochrome *c* oxidoreductase; reduced ubiquinone-cytochrome *c* oxidoreductase; mitochondrial electron transport complex III; ubiquinol-cytochrome *c*-2 oxidoreductase; ubiquinone-cytochrome *b*-*c*1 oxidoreductase; ubiquinol-cytochrome *c*₂ reductase; ubiquinol-cytochrome *c*₁ oxidoreductase; CoQH₂-cytochrome *c* oxidoreductase; ubihydroquinol:cytochrome *c* oxidoreductase; coenzyme QH₂-cytochrome *c* reductase; QH₂:cytochrome *c* oxidoreductase; ubiquinol:ferricytochrome-*c* oxidoreductase

Systematic name: quinol:ferricytochrome-*c* oxidoreductase

Comments: The enzyme, often referred to as the cytochrome *bc*₁ complex or complex III, is the third complex in the electron transport chain. It is present in the mitochondria of all aerobic eukaryotes and in the inner membranes of most bacteria. The mammalian enzyme contains cytochromes *b*-562, *b*-566 and *c*1, and a 2-iron ferredoxin. Depending on the organism and physiological conditions, the enzyme extrudes either two or four protons from the cytoplasmic to the non-cytoplasmic compartment (*cf.* EC 1.6.99.3, NADH dehydrogenase).

References: [162, 208, 275, 237, 284, 71]

[EC 7.1.1.8 created 1978 as EC 1.10.2.2, modified 2013, transferred 2018 to EC 7.1.1.8]

EC 7.1.1.9

Accepted name: cytochrome-*c* oxidase

Reaction: 4 ferrocycytochrome *c* + O₂ + 8 H⁺_[side 1] = 4 ferricytochrome *c* + 2 H₂O + 4 H⁺_[side 2]

Other name(s): cytochrome *aa*₃; cytochrome *caa*₃; cytochrome *bb*₃; cytochrome *cbb*₃; cytochrome *ba*₃; cytochrome *a*₃; Warburg's respiratory enzyme; indophenol oxidase; indophenolase; complex IV (mitochondrial electron transport); ferrocycytochrome *c* oxidase; cytochrome oxidase (ambiguous); NADH cytochrome *c* oxidase (incorrect)

Systematic name: ferrocycytochrome-*c*:oxygen oxidoreductase

Comments: An oligomeric membrane heme-Cu:O₂ reductase-type enzyme that terminates the respiratory chains of aerobic and facultative aerobic organisms. The reduction of O₂ to water is accompanied by the extrusion of four protons. The cytochrome-*aa*₃ enzymes of mitochondria and many bacterial species are the most abundant group, but other variations, such as the bacterial cytochrome-*cbb*₃ enzymes, also exist. All of the variants have a conserved catalytic core subunit (subunit I) that contains a low-spin heme (of *a*- or *b*-type), a binuclear metal centre composed of a high-spin heme iron (of *a*-, *o*-, or *b*-type heme, referred to as *a*₃, *o*₃ or *b*₃ heme), and a Cu atom (CuB). Besides subunit I, the enzyme usually has at least two other core subunits: subunit II is the primary electron acceptor; subunit III usually does not contain any cofactors, but in the case of *cbb*₃-type enzymes it is a diheme *c*-type cytochrome. While most bacterial enzymes consist of only 3–4 subunits, the mitochondrial enzyme is much more complex and contains 14 subunits.

References: [121, 122, 266, 282, 283, 94, 120, 69]

[EC 7.1.1.9 created 1961 as EC 1.9.3.1, modified 2000, transferred 2019 to EC 7.1.1.9, modified 2021]

EC 7.1.1.10

Accepted name: ferredoxin—quinone oxidoreductase (H⁺-translocating)

Reaction: 2 reduced ferredoxin [iron-sulfur] cluster + plastoquinone + 6 H⁺_[side 1] = 2 oxidized ferredoxin [iron-sulfur] cluster + plastoquinol + 7 H⁺_[side 2]

Other name(s): NDH-1L complex; NDH-1L' complex; NDH₁ complex; NDH₂ complex

Systematic name: ferredoxin:quinone oxidoreductase (H⁺-translocating)

Comments: The enzyme, present in plants and cyanobacteria, couples electron transport from ferredoxin to plastoquinone and proton pumping from the cytoplasm to the thylakoid lumen. It participates in cyclic electron flow, retuning electrons generated by photosystem I to the plastoquinone pool, thus bypassing the generation of reducing power. It may also participate in respiration using electrons originating from NADPH via the action of EC 1.18.1.2, ferredoxin—NADP⁺ reductase (FNR) operating in the direction of ferredoxin reduction. It is a large complex, with some of its subunits resembling those from the bacterial/mitochondrial EC 7.1.1.2, NADH:ubiquinone reductase (H⁺-translocating). However, it lacks the NADH-oxidizing module and instead has a module that interacts with ferredoxin. Several forms of the enzyme exist, differing in their exact combination of subunits used. Some of the forms participate in carbon dioxide hydration rather than electron transfer.

References: [7, 17, 279, 152, 192, 137, 219, 286]

[EC 7.1.1.10 created 2021]

EC 7.1.1.11

Accepted name: ferredoxin—NAD⁺ oxidoreductase (H⁺-transporting)

Reaction: 2 reduced ferredoxin [iron-sulfur] cluster + NAD⁺ + H⁺ + 2 H⁺_[side 1] = 2 oxidized ferredoxin [iron-sulfur] cluster + NADH + 2 H⁺_[side 2]

Other name(s): Rnf complex (ambiguous); H⁺-translocating ferredoxin:NAD⁺ oxidoreductase

Systematic name: ferredoxin:NAD⁺ oxidoreductase (H⁺-transporting)

Comments: This iron-sulfur and flavin-containing electron transport complex, isolated from some anaerobic bacteria, couples the energy from reduction of NAD⁺ by ferredoxin to pumping protons out of the cell, generating a proton motive force across the cytoplasmic membrane. Most similar complexes pump sodium ions rather than protons [*cf.* EC 7.2.1.2, ferredoxin—NAD⁺ oxidoreductase (Na⁺-transporting)].

References: [257, 268]

[EC 7.1.1.11 created 2021]

EC 7.1.1.12

Accepted name: succinate dehydrogenase (electrogenic, proton-motive force generating)

Reaction: succinate + menaquinone + 2 H⁺_[side 1] = fumarate + menaquinol + 2 H⁺_[side 2]

Systematic name: succinate:quinone oxidoreductase (electrogenic, proton-motive force generating)
Comments: The enzyme is very similar to EC 1.3.5.1, succinate dehydrogenase, but differs by containing two heme molecules (located in the membrane anchor component) in addition to FAD and three iron-sulfur clusters. Unlike EC 1.3.5.1, this enzyme catalyses an electrogenic reaction, enabled by electron-bifurcation via the heme molecules. In the direction of succinate oxidation by menaquinone, which is endergonic, the reaction is driven by the transmembrane electrochemical proton potential. In the direction of fumarate reduction, the electrogenic electron transfer reaction is compensated by transmembrane proton transfer pathway known as the E-pathway, which results in overall electroneutrality.
References: [134, 155, 136, 135, 88]

[EC 7.1.1.12 created 2022]

EC 7.1.2 Linked to the hydrolysis of a nucleoside triphosphate

EC 7.1.2.1

Accepted name: P-type H⁺-exporting transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{H}^+_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{H}^+_{[\text{side 2}]}$
Other name(s): proton-translocating ATPase; yeast plasma membrane H⁺-ATPase; yeast plasma membrane ATPase; ATP phosphohydrolase (ambiguous); proton-exporting ATPase; proton transport ATPase; proton-translocating P-type ATPase; H⁺-transporting ATPase
Systematic name: ATP phosphohydrolase (P-type, 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: [84, 223, 224, 193]

[EC 7.1.2.1 created 1984 as EC 3.6.1.35, transferred 2000 to EC 3.6.3.6, transferred 2018 to EC 7.1.2.1]

EC 7.1.2.2

Accepted name: H⁺-transporting two-sector ATPase
Reaction: $\text{ATP} + \text{H}_2\text{O} + 4 \text{H}^+_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + 4 \text{H}^+_{[\text{side 2}]}$
Other name(s): ATP synthase; F₁-ATPase; F_oF₁-ATPase; H⁺-transporting ATPase; mitochondrial ATPase; coupling factors (F_o F₁ and CF1); chloroplast ATPase; bacterial Ca²⁺/Mg²⁺ ATPase
Systematic name: ATP phosphohydrolase (two-sector, 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 (F_o, V_o, A_o) 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 (archaeal) enzymes have a similar structure but, under physiological conditions, they pump H⁺ rather than synthesize ATP.
References: [193, 42, 2, 36, 183, 259]

[EC 7.1.2.2 created 1984 as EC 3.6.1.34, transferred 2000 to EC 3.6.3.14, transferred 2018 to EC 7.1.2.2]

EC 7.1.3 Linked to the hydrolysis of diphosphate

EC 7.1.3.1

Accepted name: H⁺-exporting diphosphatase
Reaction: diphosphate + H₂O + H⁺_[side 1] = 2 phosphate + H⁺_[side 2]
Other name(s): H⁺-PPase; proton-pumping pyrophosphatase; vacuolar H⁺-pyrophosphatase; hydrogen-translocating pyrophosphatase; proton-pumping dihydrophatase
Systematic name: diphosphate phosphohydrolase (H⁺-transporting)
Comments: This enzyme, found in plants and fungi, couples the energy from diphosphate hydrolysis to active proton translocation across the tonoplast into the vacuole. The enzyme acts cooperatively with cytosolic soluble diphosphatases to regulate the cytosolic diphosphate level.
References: [205, 215, 92, 222]

[EC 7.1.3.1 created 2018]

[7.1.3.2 *Transferred entry. Na⁺-exporting diphosphatase. Now EC 7.2.3.1, Na⁺-exporting diphosphatase*]

[EC 7.1.3.2 created 2021, deleted 2022]

EC 7.2 Catalysing the translocation of inorganic cations

This subclass contains translocases that transfer inorganic cations (metal cations). Subclasses are based on the reaction processes that provide the driving force for the translocation. 7.2.1 Translocation of inorganic cations linked to oxidoreductase reactions. 7.2.2 Translocation of inorganic cations linked to the hydrolysis of a nucleoside triphosphate. 7.2.4 Translocation of inorganic cations linked to decarboxylation reactions.

EC 7.2.1 Linked to oxidoreductase reactions

EC 7.2.1.1

Accepted name: NADH:ubiquinone reductase (Na⁺-transporting)
Reaction: NADH + H⁺ + ubiquinone + *n* Na⁺_[side 1] = NAD⁺ + ubiquinol + *n* Na⁺_[side 2]
Other name(s): Na⁺-translocating NADH-quinone reductase; Na⁺-NQR
Systematic name: NADH:ubiquinone oxidoreductase (Na⁺-translocating)
Comments: An iron-sulfur flavoprotein, containing two covalently bound molecules of FMN, one noncovalently bound FAD, one riboflavin, and one [2Fe-2S] cluster.
References: [19, 179, 37, 15, 16]

[EC 7.2.1.1 created 2011 as EC 1.6.5.8, transferred 2018 to EC 7.2.1.1]

EC 7.2.1.2

Accepted name: ferredoxin—NAD⁺ oxidoreductase (Na⁺-transporting)
Reaction: 2 reduced ferredoxin [iron-sulfur] cluster + NAD⁺ + H⁺ + Na⁺_[side 1] = 2 oxidized ferredoxin [iron-sulfur] cluster + NADH + Na⁺_[side 2]
Other name(s): Rnf complex (ambiguous); Na⁺-translocating ferredoxin:NAD⁺ oxidoreductase
Systematic name: ferredoxin:NAD⁺ oxidoreductase (Na⁺-transporting)
Comments: This iron-sulfur and flavin-containing electron transport complex, isolated from the bacterium *Acetobacterium woodii*, couples the energy from reduction of NAD⁺ by ferredoxin to pumping sodium ions out of the cell, generating a gradient across the cytoplasmic membrane.
References: [33, 32, 97]

[EC 7.2.1.2 created 2015 as EC 1.18.1.8, transferred 2018 to EC 7.2.1.2]

EC 7.2.1.3

Accepted name: ascorbate ferrireductase (transmembrane)
Reaction: ascorbate_[side 1] + Fe(III)_[side 2] = monodehydroascorbate_[side 1] + Fe(II)_[side 2]
Other name(s): cytochrome *b*₅₆₁ (ambiguous)
Systematic name: Fe(III):ascorbate oxidoreductase (electron-translocating)
Comments: A diheme cytochrome that transfers electrons across a single membrane, such as the outer membrane of the enterocyte, or the tonoplast membrane of the plant cell vacuole. Acts on hexacyanoferrate(III) and other ferric chelates.
References: [75, 165, 244, 26, 277, 81]

[EC 7.2.1.3 created 2011 as EC 1.16.5.1, transferred 2018 to EC 7.2.1.3]

EC 7.2.2 Linked to the hydrolysis of a nucleoside triphosphate

EC 7.2.2.1

Accepted name: Na⁺-transporting two-sector ATPase
Reaction: ATP + H₂O + *n* Na⁺_[side 1] = ADP + phosphate + *n* Na⁺_[side 2]
Other name(s): sodium-transporting two-sector ATPase; Na⁺-translocating ATPase; Na⁺-translocating F₀F₁-ATPase; sodium ion specific ATP synthase
Systematic name: ATP phosphohydrolase (two-sector, Na⁺-transporting)
Comments: A multisubunit ATPase transporter found in some halophilic or alkalophilic bacteria that functions in maintaining sodium homeostasis. The enzyme is similar to EC 7.1.2.2 (H⁺-transporting two-sector ATPase) but pumps Na⁺ rather than H⁺. By analogy to EC 7.1.2.2, it is likely that the enzyme pumps 4 sodium ions for every ATP molecule that is hydrolysed. *cf.* EC 7.2.2.3, P-type Na⁺ transporter and EC 7.2.2.4, ABC-type Na⁺ transporter.
References: [236, 250, 203]

[EC 7.2.2.1 created 2000 as EC 3.6.3.15, transferred 2018 to EC 7.2.2.1, modified 2018]

EC 7.2.2.2

Accepted name: ABC-type Cd²⁺ transporter
Reaction: ATP + H₂O + Cd²⁺_[side 1] = ADP + phosphate + Cd²⁺_[side 2]
Other name(s): cadmium-transporting ATPase (ambiguous); ABC-type cadmium-transporter
Systematic name: ATP phosphohydrolase (ABC-type, heavy-metal-exporting)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. Does not undergo phosphorylation during the transport process. A yeast enzyme that exports some heavy metals, especially Cd²⁺, from the cytosol into the vacuole.
References: [146, 213]

[EC 7.2.2.2 created 2000 as EC 3.6.3.46, transferred 2018 to EC 7.2.2.2]

EC 7.2.2.3

Accepted name: P-type Na⁺ transporter
Reaction: ATP + H₂O + Na⁺_[side 1] = ADP + phosphate + Na⁺_[side 2]
Other name(s): Na⁺-exporting ATPase (ambiguous); ENA1 (gene name); ENA2 (gene name); ENA5 (gene name); sodium transport ATPase (ambiguous); sodium-translocating P-type ATPase
Systematic name: ATP phosphohydrolase (P-type, 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. Some forms can also export Li⁺ ions. *cf.* EC 7.2.2.1, Na⁺-transporting two-sector ATPase and EC 7.2.2.4, ABC-type Na⁺ transporter.
References: [273, 50, 25, 213]

[EC 7.2.2.3 created 2000 as EC 3.6.3.7, modified 2001, transferred 20018 to EC 7.2.2.3]

EC 7.2.2.4

Accepted name: ABC-type Na⁺ transporter
Reaction: ATP + H₂O + Na⁺_[side 1] = ADP + phosphate + Na⁺_[side 2]
Other name(s): *natAB* (gene names)
Systematic name: ATP phosphohydrolase (ABC-type, Na⁺-exporting)
Comments: ABC-type (ATP-binding cassette-type) transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. This bacterial enzyme, characterized from *Bacillus subtilis*, exports Na⁺ ions out of the cell. *cf.* EC 7.2.2.1, Na⁺-transporting two-sector ATPase and EC 7.2.2.3, P-type Na⁺ transporter.
References: [52, 185]

[EC 7.2.2.4 created 2018]

EC 7.2.2.5

Accepted name: ABC-type Mn²⁺ transporter
Reaction: ATP + H₂O + Mn²⁺-[manganese-binding protein]_[side 1] = ADP + phosphate + Mn²⁺_[side 2] + [manganese-binding protein]_[side 1]
Other name(s): ABC-type manganese permease complex; manganese-transporting ATPase (ambiguous); ABC-type manganese transporter
Systematic name: ATP phosphohydrolase (ABC-type, Mn²⁺-importing)
Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the import of Mn²⁺, Zn²⁺ and iron chelates.
References: [133, 213, 184, 130]

[EC 7.2.2.5 created 2000 as EC 3.6.3.35, transferred 2018 to EC 7.2.2.5]

EC 7.2.2.6

Accepted name: P-type K⁺ transporter
Reaction: ATP + H₂O + K⁺_[side 1] = ADP + phosphate + K⁺_[side 2]
Other name(s): K⁺-translocating Kdp-ATPase; multi-subunit K⁺-transport ATPase; K⁺-transporting ATPase; potassium-importing ATPase; K⁺-importing ATPase
Systematic name: ATP phosphohydrolase (P-type, K⁺-importing)
Comments: A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. A bacterial enzyme that is involved in K⁺ import. The probable stoichiometry is one ion per ATP hydrolysed.
References: [227, 79, 107]

[EC 7.2.2.6 created 2000 as EC 3.6.3.12, transferred 2018 to EC 7.2.2.6]

EC 7.2.2.7

Accepted name: ABC-type Fe³⁺ transporter
Reaction: ATP + H₂O + Fe³⁺-[iron-binding protein]_[side 1] = ADP + phosphate + Fe³⁺_[side 2] + [iron-binding protein]_[side 1]
Other name(s): Fe³⁺-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, Fe³⁺-transporting)
Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains. A bacterial enzyme that interacts with a periplasmic iron-binding protein to imports Fe³⁺ ions into the cytoplasm.
References: [6, 133, 213, 126]

[EC 7.2.2.7 created 2000 as EC 3.6.3.30, transferred 2018 to EC 7.2.2.7]

EC 7.2.2.8

- Accepted name:** P-type Cu⁺ transporter
Reaction: ATP + H₂O + Cu⁺_[side 1] = ADP + phosphate + Cu⁺_[side 2]
Other name(s): Cu⁺-exporting ATPase (ambiguous); *copA* (gene name); ATP7A (gene name); ATP7B (gene name)
Systematic name: ATP phosphohydrolase (P-type, Cu⁺-exporting)
Comments: A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. This enzyme transports Cu⁺ or Ag⁺, and cannot transport the divalent ions, contrary to EC 7.2.2.9, P-type Cu²⁺ transporter, which mainly transports the divalent copper ion.
References: [73, 12, 161, 85, 144, 248, 164]

[EC 7.2.2.8 created 2013 as EC 3.6.3.54, transferred 2018 to EC 7.2.2.8]

EC 7.2.2.9

- Accepted name:** P-type Cu²⁺ transporter
Reaction: ATP + H₂O + Cu²⁺_[side 1] = ADP + phosphate + Cu²⁺_[side 2]
Other name(s): Cu²⁺-exporting ATPase; *copB* (gene name)
Systematic name: ATP phosphohydrolase (P-type, Cu²⁺-exporting)
Comments: A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. The enzyme from the thermophilic archaeon *Archaeoglobus fulgidus* is involved in copper extrusion from the cell [160, 113].
References: [160, 113]

[EC 7.2.2.9 created 2000 as EC 3.6.3.4, modified 2013, transferred 2018 to EC 7.2.2.9]

EC 7.2.2.10

- Accepted name:** P-type Ca²⁺ transporter
Reaction: ATP + H₂O + Ca²⁺_[side 1] = ADP + phosphate + Ca²⁺_[side 2]
Other name(s): sarcoplasmic reticulum ATPase; sarco(endo)plasmic reticulum Ca²⁺-ATPase; calcium pump; Ca²⁺-pumping ATPase; plasma membrane Ca-ATPase; Ca²⁺-transporting ATPaseP-
Systematic name: ATP phosphohydrolase (P-type, Ca²⁺-transporting)
Comments: A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. This enzyme family comprises three types of Ca²⁺-transporting enzymes that are found in the plasma membrane, the sarcoplasmic reticulum, in yeast, and in some bacteria. The enzymes from plasma membrane and from yeast have been shown to transport one ion per ATP hydrolysed whereas those from the sarcoplasmic reticulum transport two ions per ATP hydrolysed. In muscle cells Ca²⁺ is transported from the cytosol (side 1) into the sarcoplasmic reticulum (side 2).
References: [217, 112, 48, 154, 255, 5]

[EC 7.2.2.10 created 1984 as EC 3.6.1.38, transferred 2000 to EC 3.6.3.8, modified 2001, modified 2011, transferred 2018 to EC 7.2.2.10]

EC 7.2.2.11

- Accepted name:** ABC-type Ni²⁺ transporter
Reaction: ATP + H₂O + Ni²⁺-[nickel-binding protein]_[side 1] = ADP + phosphate + Ni²⁺_[side 2] + [nickel-binding protein]_[side 1]
Other name(s): nickel ABC transporter; nickel-transporting ATPase; ABC-type nickel-transporter
Systematic name: ATP phosphohydrolase (ABC-type, Ni²⁺-importing)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the high affinity uptake of Ni²⁺; the identity of the nickel species transported has not been conclusively established. Does not undergo phosphorylation during the transport process.
References: [133, 93, 213, 86]

[EC 7.2.2.11 created 2000 as EC 3.6.3.24, transferred 2018 to EC 7.2.2.11]

EC 7.2.2.12

- Accepted name:** P-type Zn²⁺ transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{Zn}^{2+}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{Zn}^{2+}_{[\text{side 2}]}$
Other name(s): Zn(II)-translocating P-type ATPase; Zn²⁺-exporting ATPase; P1B-type ATPase; HMA4 (gene name); *zntA* (gene name)
Systematic name: ATP phosphohydrolase (P-type, Zn²⁺-exporting)
Comments: A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. The enzyme, present in prokaryotes and photosynthetic eukaryotes, exports Zn²⁺ and the related cations Cd²⁺ and Pb²⁺.
References: [18, 206, 207, 172, 72]

[EC 7.2.2.12 created 2000 as EC 3.6.3.5, modified 2001, modified 2006, transferred 2018 to EC 7.2.2.12]

EC 7.2.2.13

- Accepted name:** Na⁺/K⁺-exchanging ATPase
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{Na}^{+}_{[\text{side 1}]} + \text{K}^{+}_{[\text{side 2}]} = \text{ADP} + \text{phosphate} + \text{Na}^{+}_{[\text{side 2}]} + \text{K}^{+}_{[\text{side 1}]}$
Other name(s): (Na⁺ + K⁺)-activated ATPase; Na,K-activated ATPase; Na,K-pump; Na⁺,K⁺-ATPase; sodium/potassium-transporting ATPase; Na⁺/K⁺-exchanging ATPase
Systematic name: ATP phosphohydrolase (P-type, 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: [232, 197, 233, 49]

[EC 7.2.2.13 created 1984 EC 3.6.1.37, transferred 2000 to EC 3.6.3.9, modified 2001, transferred 2018 to EC 7.2.2.13]

EC 7.2.2.14

- Accepted name:** P-type Mg²⁺ transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{Mg}^{2+}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{Mg}^{2+}_{[\text{side 2}]}$
Other name(s): Mg²⁺-transporting P-type ATPase; Mg²⁺-transporting ATPase; Mg²⁺-importing ATPase; magnesium-translocating P-type ATPase; *mgtA* (gene name); *mgtB* (gene name)
Systematic name: ATP phosphohydrolase (P-type, Mg²⁺-importing)
Comments: A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. A bacterial enzyme that imports Mg²⁺ with, rather than against, the Mg²⁺ electrochemical gradient. The enzyme is also involved in Ni²⁺ import.
References: [235, 156, 251]

[EC 7.2.2.14 created 2000 as EC 3.6.3.2, modified 2001, transferred 2018 to EC 7.2.2.14]

EC 7.2.2.15

- Accepted name:** P-type Ag⁺ transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{Ag}^{+}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{Ag}^{+}_{[\text{side 2}]}$
Other name(s): Ag⁺-exporting ATPase
Systematic name: ATP phosphohydrolase (P-type, Ag⁺-exporting)
Comments: A P-type ATPase that exports Ag⁺ ions from some bacteria, archaea as well as from some animal tissues. The proteins also transport Cu⁺ ions (*cf.* EC 7.2.2.8, P-type Cu⁺ transporter).
References: [89, 47]

[EC 7.2.2.15 created 2000 as EC 3.6.3.53, transferred 2018 to EC 7.2.2.15]

EC 7.2.2.16

- Accepted name:** ABC-type ferric hydroxamate transporter

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{Fe}^{3+}\text{-hydroxamate complex-[hydroxamate-binding protein]}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{Fe}^{3+}\text{-hydroxamate complex}_{[\text{side 2}]} + [\text{hydroxamate-binding protein}]_{[\text{side 1}]}$

Other name(s): iron(III) hydroxamate transporting ATPase; iron(III) hydroxamate ABC transporter; *fhuCDB* (gene names)

Systematic name: ATP phosphohydrolase [ABC-type, iron(III) hydroxamate-importing]

Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the import of Fe^{3+} -complexed hydroxamate siderophores such as coprogen, ferrichrome and the ferric hydroxamate antibiotic, albomycin.

References: [132, 240]

[EC 7.2.2.16 created 2000 as EC 3.6.3.34, part transferred 2018 to EC 7.2.2.16]

EC 7.2.2.17

Accepted name: ABC-type ferric enterobactin transporter

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{Fe}^{3+}\text{-enterobactin complex-[enterobactin-binding protein]}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{Fe}^{3+}\text{-enterobactin complex}_{[\text{side 2}]} + [\text{enterobactin-binding protein}]_{[\text{side 1}]}$

Other name(s): ferric enterobactin transporting ATPase; ferric enterobactin ABC transporter; *fepBCDG* (gene names)

Systematic name: ATP phosphohydrolase (ABC-type, iron(III) enterobactin-importing)

Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the high affinity uptake of Fe^{3+} -enterobactin complexes.

References: [51, 225]

[EC 7.2.2.17 created 2000 as EC 3.6.3.34, part transferred 2018 to EC 7.2.2.17]

EC 7.2.2.18

Accepted name: ABC-type ferric citrate transporter

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{Fe}^{3+}\text{-dicitrate-[dicitrate-binding protein]}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{Fe}^{3+}\text{-dicitrate}_{[\text{side 2}]} + [\text{dicitrate-binding protein}]_{[\text{side 1}]}$

Other name(s): ferric citrate transporting ATPase; ferric citrate ABC transporter; *fecBCDE* (gene names)

Systematic name: ATP phosphohydrolase (ABC-type, iron(III) dicitrate-importing)

Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme from *Escherichia coli* interacts with a periplasmic substrate binding protein and mediates the high affinity uptake of Fe^{3+} -citrate in the form of a mononuclear (containing one iron(III) ion and two citrate molecules) or dinuclear (containing 2 iron(III) ions) complexes.

References: [241, 14]

[EC 7.2.2.18 created 2000 as EC 3.6.3.34, part transferred 2018 to EC 7.2.2.18]

EC 7.2.2.19

Accepted name: H^+/K^+ -exchanging ATPase

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{H}^+_{[\text{side 1}]} + \text{K}^+_{[\text{side 2}]} = \text{ADP} + \text{phosphate} + \text{H}^+_{[\text{side 2}]} + \text{K}^+_{[\text{side 1}]}$

Other name(s): H^+/K^+ -ATPase; H,K-ATPase; $(\text{K}^+ + \text{H}^+)\text{-ATPase}$

Systematic name: ATP phosphohydrolase (P-type, 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: [211, 95, 202]

[EC 7.2.2.19 created 1984 as EC 3.6.1.36, transferred 2000 to EC 3.6.3.10, transferred 2018 to EC 7.2.2.19]

EC 7.2.2.20

- Accepted name:** ABC-type Zn²⁺ transporter
Reaction: ATP + H₂O + Zn²⁺-[zinc-binding protein]_[side 1] = ADP + phosphate + Zn²⁺_[side 2] + [zinc-binding protein]_[side 1]
Other name(s): Zn²⁺-transporting ATPase; Zn²⁺ ABC transporter; *znuABC* (gene names)
Systematic name: ATP phosphohydrolase (ABC-type, Zn²⁺-importing)
Comments: ABC-type (ATP-binding cassette-type) transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the high-affinity import of Zn²⁺.
References: [189, 90]

[EC 7.2.2.20 created 2019]

EC 7.2.2.21

- Accepted name:** Cd²⁺-exporting ATPase
Reaction: ATP + H₂O + Cd²⁺_[side 1] = ADP + phosphate + Cd²⁺_[side 2]
Other name(s): cadmium-translocating P-type ATPase; cadmium-exporting ATPase
Systematic name: ATP phosphohydrolase (Cd²⁺-exporting)
Comments: A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. This enzyme occurs in protozoa, fungi and plants.
References: [228, 258]

[EC 7.2.2.21 created 2000 as EC 3.6.3.3, transferred 2019 to EC 7.2.2.21]

EC 7.2.2.22

- Accepted name:** P-type Mn²⁺ transporter
Reaction: ATP + H₂O + Mn²⁺_[side 1] = ADP + phosphate + Mn²⁺_[side 2]
Other name(s): Mn(II)-translocating P-type ATPase; Mn²⁺-exporting ATPase; P1B-type ATPase (ambiguous); *ctpC* (gene name)
Systematic name: ATP phosphohydrolase (P-type, Mn²⁺-exporting)
Comments: A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. The enzyme, detected in mycobacteria, is a high affinity slow turnover ATPase exporting Mn²⁺.
References: [188]

[EC 7.2.2.22 created 2021]

EC 7.2.3 Linked to the hydrolysis of a nucleoside triphosphate

EC 7.2.3.1

- Accepted name:** Na⁺-exporting diphosphatase
Reaction: diphosphate + H₂O + Na⁺_[side 1] = 2 phosphate + Na⁺_[side 2]
Other name(s): Na⁺-translocating membrane pyrophosphatase; sodium-translocating pyrophosphatase
Systematic name: diphosphate phosphohydrolase (Na⁺-transporting)
Comments: Requires Na⁺ and K⁺. This enzyme, found in some bacteria and archaea, couples the energy from diphosphate hydrolysis to active sodium translocation across the membrane. The enzyme is electrogenic, as the Na⁺ transport results in generation of a positive potential in the inner side of the membrane.
References: [24, 159, 151]

[EC 7.2.3.1 created 2021 as EC 7.1.3.2, transferred 2022 to EC 7.2.3.1]

EC 7.2.4 Linked to decarboxylation

EC 7.2.4.1

- Accepted name:** carboxybiotin decarboxylase
Reaction: a carboxybiotinyl-[protein] + $n \text{ Na}^+$ [side 1] + H^+ [side 2] = CO_2 + a biotinyl-[protein] + $n \text{ Na}^+$ [side 2] ($n = 1-2$)
Other name(s): MadB; carboxybiotin protein decarboxylase
Systematic name: carboxybiotinyl-[protein] carboxy-lyase
Comments: The integral membrane protein MadB from the anaerobic bacterium *Malonomonas rubra* is a component of the multienzyme complex EC 4.1.1.89, biotin-dependent malonate decarboxylase. The free energy of the decarboxylation reaction is used to pump Na^+ out of the cell. The enzyme is a member of the Na^+ -translocating decarboxylase family, other members of which include EC 7.2.4.2 [oxaloacetate decarboxylase (Na^+ extruding)] and EC 7.2.4.3 [(*S*)-methylmalonyl-CoA decarboxylase (sodium-transporting)] [67].
References: [28, 67]

[EC 7.2.4.1 created 2008 as EC 4.3.99.2, transferred 2018 to EC 7.2.4.1]

EC 7.2.4.2

- Accepted name:** oxaloacetate decarboxylase (Na^+ extruding)
Reaction: oxaloacetate + 2 Na^+ [side 1] = pyruvate + CO_2 + 2 Na^+ [side 2]
Other name(s): oxaloacetate β -decarboxylase (ambiguous); oxalacetic acid decarboxylase (ambiguous); oxalate β -decarboxylase (ambiguous); oxaloacetate carboxy-lyase (ambiguous)
Systematic name: oxaloacetate carboxy-lyase (pyruvate-forming; Na^+ -extruding)
Comments: The enzyme from the bacterium *Klebsiella aerogenes* is a biotinyl protein and also decarboxylates glutaconyl-CoA and methylmalonyl-CoA. The process is accompanied by the extrusion of two sodium ions from cells. Some animal enzymes require Mn^{2+} . Differs from EC 4.1.1.112 (oxaloacetate decarboxylase) for which there is no evidence for involvement in Na^+ transport.
References: [65, 66]

[EC 7.2.4.2 created 1961 as EC 4.1.1.3, modified 1986, modified 2000, transferred 2018 to EC 7.2.4.2]

EC 7.2.4.3

- Accepted name:** (*S*)-methylmalonyl-CoA decarboxylase (sodium-transporting)
Reaction: (*S*)-methylmalonyl-CoA + Na^+ [side 1] + H^+ [side 2] = propanoyl-CoA + CO_2 + Na^+ [side 2]
Other name(s): methylmalonyl-coenzyme A decarboxylase (ambiguous); (*S*)-2-methyl-3-oxopropanoyl-CoA carboxy-lyase (incorrect); (*S*)-methylmalonyl-CoA carboxy-lyase (ambiguous)
Systematic name: (*S*)-methylmalonyl-CoA carboxy-lyase (propanoyl-CoA-forming, sodium-transporting)
Comments: This bacterial enzyme couples the decarboxylation of (*S*)-methylmalonyl-CoA to propanoyl-CoA to the vectorial transport of Na^+ across the cytoplasmic membrane, thereby creating a sodium ion motive force that is used for ATP synthesis. It is a membrane-associated biotin protein and is strictly dependent on sodium ions for activity.
References: [78, 102, 103, 108, 41]

[EC 7.2.4.3 created 1972 as EC 4.1.1.41, modified 1983, modified 1986, transferred 2018 to EC 7.2.4.3]

EC 7.2.4.4

- Accepted name:** biotin-dependent malonate decarboxylase
Reaction: malonate + H^+ + Na^+ [side 1] = acetate + CO_2 + Na^+ [side 2]
Other name(s): malonate decarboxylase (with biotin); malonate decarboxylase (ambiguous)
Systematic name: malonate carboxy-lyase (biotin-dependent)

Comments: Two types of malonate decarboxylase are currently known, both of which form multienzyme complexes. The enzyme described here is a membrane-bound biotin-dependent, Na⁺-translocating enzyme [128]. The other type is a biotin-independent cytosolic protein (*cf.* EC 4.1.1.88, biotin-independent malonate decarboxylase). As free malonate is chemically rather inert, it has to be activated prior to decarboxylation. Both enzymes achieve this by exchanging malonate with an acetyl group bound to an acyl-carrier protein (ACP), to form malonyl-ACP and acetate, with subsequent decarboxylation regenerating the acetyl-bound form of the enzyme. The ACP subunit of both enzymes differs from that found in fatty-acid biosynthesis by having phosphopantetheine attached to a serine side-chain as 2-(5-triphosphoribosyl)-3-dephospho-CoA rather than as phosphopantetheine 4'-phosphate. In the anaerobic bacterium *Malonomonas rubra*, the components of the multienzyme complex/enzymes involved in carrying out the reactions of this enzyme are as follows: MadA (EC 2.3.1.187, acetyl-S-ACP:malonate ACP transferase), MadB (EC 7.2.4.1, carboxybiotin decarboxylase), MadC/MadD (EC 2.1.3.10, malonyl-S-ACP:biotin-protein carboxyltransferase) and MadH (EC 6.2.1.35, acetate—[acyl-carrier protein] ligase). Two other components that are involved are MadE, the acyl-carrier protein and MadF, the biotin protein. The carboxy group is lost with retention of configuration [170].

References: [100, 101, 27, 28, 170, 128, 67]

[EC 7.2.4.4 created 2008 as EC 4.1.1.89, transferred 2018 to EC 7.2.4.4]

EC 7.2.4.5

Accepted name: glutaconyl-CoA decarboxylase

Reaction: (2*E*)-4-carboxybut-2-enoyl-CoA + Na⁺_[side 1] = (2*E*)-but-2-enoyl-CoA + CO₂ + Na⁺_[side 2]

Other name(s): glutaconyl coenzyme A decarboxylase; pent-2-enoyl-CoA carboxy-lyase; 4-carboxybut-2-enoyl-CoA carboxy-lyase

Systematic name: (2*E*)-4-carboxybut-2-enoyl-CoA carboxy-lyase [(2*E*)-but-2-enoyl-CoA-forming]

Comments: The enzyme from the bacterium *Acidaminococcus fermentans* is a biotinyl-protein, requires Na⁺, and acts as a sodium pump. Prior to the Na⁺-dependent decarboxylation, the carboxylate is transferred to biotin in a Na⁺-independent manner. The conserved lysine, to which biotin forms an amide bond, is located 34 amino acids before the C-terminus, flanked on both sides by two methionine residues, which are conserved in every biotin-dependent enzyme.

References: [46, 45]

[EC 7.2.4.5 created 1986 as EC 4.1.1.70, modified 2003, transferred 2019 to EC 7.2.4.5]

EC 7.3 Catalysing the translocation of inorganic anions and their chelates

This subclass contains translocases that transfer inorganic cations anions and their chelates. Subclasses are based on the reaction processes that provide the driving force for the translocation. At present only one subclass is represented: EC 7.3.2 Translocation of inorganic anions and their chelates linked to the hydrolysis of a nucleoside triphosphate.

EC 7.3.2 Linked to the hydrolysis of a nucleoside triphosphate

EC 7.3.2.1

Accepted name: ABC-type phosphate transporter

Reaction: ATP + H₂O + phosphate-[phosphate-binding protein]_[side 1] = ADP + phosphate + phosphate_[side 2] + [phosphate-binding protein]_[side 1]

Other name(s): phosphate ABC transporter; phosphate-transporting ATPase (ambiguous)

Systematic name: ATP phosphohydrolase (ABC-type, phosphate-importing)

Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the high affinity uptake of phosphate anions. Unlike P-type ATPases, it does not undergo phosphorylation during the transport process.

References: [270, 133, 43, 213, 86]

[EC 7.3.2.1 created 2000 as EC 3.6.3.27, transferred 2018 to EC 7.3.2.1]

EC 7.3.2.2

Accepted name: ABC-type phosphonate transporter

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{phosphonate-}[\text{phosphonate-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{phosphonate}_{[\text{side 2}]} + [\text{phosphonate-binding protein}]_{[\text{side 1}]}$

Other name(s): phosphonate-transporting ATPase (ambiguous)

Systematic name: ATP phosphohydrolase (ABC-type, phosphonate-importing)

Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme, found in bacteria, interacts with an extracytoplasmic substrate binding protein and mediates the import of phosphonate and organophosphate anions.

References: [269, 133, 213, 86]

[EC 7.3.2.2 created 2000 as EC 3.6.3.28, transferred 2018 to EC 7.3.2.2]

EC 7.3.2.3

Accepted name: ABC-type sulfate transporter

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{sulfate-}[\text{sulfate-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{sulfate}_{[\text{side 2}]} + [\text{sulfate-binding protein}]_{[\text{side 1}]}$

Other name(s): sulfate ABC transporter; sulfate-transporting ATPase (ambiguous)

Systematic name: ATP phosphohydrolase (ABC-type, sulfate-importing)

Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme from *Escherichia coli* can interact with either of two periplasmic binding proteins and mediates the high affinity uptake of sulfate and thiosulfate. May also be involved in the uptake of selenite, selenate and possibly molybdate. Does not undergo phosphorylation during the transport.

References: [231, 133, 213]

[EC 7.3.2.3 created 2000 as EC 3.6.3.25, transferred 2018 to EC 7.3.2.3]

EC 7.3.2.4

Accepted name: ABC-type nitrate transporter

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{nitrate-}[\text{nitrate-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{nitrate}_{[\text{side 2}]} + [\text{nitrate-binding protein}]_{[\text{side 1}]}$

Other name(s): nitrate-transporting ATPase (ambiguous)

Systematic name: ATP phosphohydrolase (ABC-type, nitrate-importing)

Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme, found in bacteria, interacts with an extracytoplasmic substrate binding protein and mediates the import of nitrate, nitrite, and cyanate.

References: [187, 133, 213, 86]

[EC 7.3.2.4 created 2000 as EC 3.6.3.26, transferred 2018 to EC 7.3.2.4]

EC 7.3.2.5

- Accepted name:** ABC-type molybdate transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{molybdate-}[\text{molybdate-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{molybdate}_{[\text{side 2}]} + [\text{molybdate-binding protein}]_{[\text{side 1}]}$
Other name(s): molybdate ABC transporter; molybdate-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, molybdate-importing)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme, found in bacteria, interacts with an extracytoplasmic substrate binding protein and mediates the high-affinity import of molybdate and tungstate. Does not undergo phosphorylation during the transport process.
References: [133, 87, 213, 86]

[EC 7.3.2.5 created 2000 as EC 3.6.3.29, transferred 2018 to EC 7.3.2.5]

EC 7.3.2.6

- Accepted name:** ABC-type tungstate transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{tungstate-}[\text{tungstate-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{tungstate}_{[\text{side 2}]} + [\text{tungstate-binding protein}]_{[\text{side 1}]}$
Other name(s): tungstate transporter; tungstate-importing ATPase; tungstate-specific ABC transporter; WtpABC; TupABC
Systematic name: ATP phosphohydrolase (ABC-type, tungstate-importing)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme, characterized from the archaeon *Pyrococcus furiosus*, the Gram-positive bacterium *Eubacterium acidaminophilum* and the Gram-negative bacterium *Campylobacter jejuni*, interacts with an extracytoplasmic substrate binding protein and mediates the import of tungstate into the cell for incorporation into tungsten-dependent enzymes.
References: [158, 31, 234]

[EC 7.3.2.6 created 2013 as EC 3.6.3.55, transferred 2018 to EC 7.3.2.6]

EC 7.3.2.7

- Accepted name:** arsenite-transporting ATPase
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{arsenite}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{arsenite}_{[\text{side 2}]}$
Other name(s): *arsAB* (gene names)
Systematic name: ATP phosphohydrolase (arsenite-exporting)
Comments: This bacterial transporter does not belong to the ABC superfamily, and instead is a member of its own family, referred to as the Ars family. The enzyme 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. It forms an arsenite efflux pump that removes arsenite from the cytoplasm, and can also remove antimonite anions.
References: [229, 209, 44, 288]

[EC 7.3.2.7 created 2000 as EC 3.6.3.16, transferred 2019 to EC 7.3.2.7]

EC 7.4 Catalysing the translocation of amino acids and peptides

Subclasses are based on the reaction processes that provide the driving force for the translocation. At present there is only one subclass: EC 7.4.2 Translocation of amino acids and peptides linked to the hydrolysis of a nucleoside triphosphate.

EC 7.4.2 Linked to the hydrolysis of a nucleoside triphosphate

EC 7.4.2.1

- Accepted name:** ABC-type polar-amino-acid transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{polar amino acid} \cdot [\text{polar amino acid-binding protein}]_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{polar amino acid}_{[\text{side } 2]} + [\text{polar amino acid-binding protein}]_{[\text{side } 1]}$
Other name(s): histidine permease; polar-amino-acid-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, polar-amino-acid-importing)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme, found in bacteria, interacts with an extracytoplasmic substrate binding protein and mediates the import of polar amino acids. This entry comprises bacterial enzymes that import His, Arg, Lys, Glu, Gln, Asp, ornithine, octopine and nopaline.
References: [133, 182, 267, 213]

[EC 7.4.2.1 created 2000 as EC 3.6.3.21, transferred 2018 to EC 7.4.2.1]

EC 7.4.2.2

- Accepted name:** ABC-type nonpolar-amino-acid transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{nonpolar amino acid} \cdot [\text{nonpolar amino acid-binding protein}]_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{nonpolar amino acid}_{[\text{side } 2]} + [\text{nonpolar amino acid-binding protein}]_{[\text{side } 1]}$
Other name(s): nonpolar-amino-acid-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, nonpolar-amino-acid-importing)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme, found in bacteria, interacts with an extracytoplasmic substrate binding protein. This entry comprises enzymes that import Leu, Ile and Val.
References: [133, 213, 86]

[EC 7.4.2.2 created 2000 as EC 3.6.3.22, transferred 2018 to EC 7.4.2.2]

EC 7.4.2.3

- Accepted name:** mitochondrial protein-transporting ATPase
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{mitochondrial-protein}_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{mitochondrial-protein}_{[\text{side } 2]}$
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 mitochondrial inner 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: [38, 30, 264]

[EC 7.4.2.3 created 2000 as EC 3.6.3.51, transferred 2018 to EC 7.4.2.3]

EC 7.4.2.4

- Accepted name:** chloroplast protein-transporting ATPase
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{chloroplast-protein}_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{chloroplast-protein}_{[\text{side } 2]}$
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: [59, 178, 220]

[EC 7.4.2.4 created 2000 as EC 3.6.3.52, transferred 2018 to EC 7.4.2.4]

EC 7.4.2.5

Accepted name: bacterial ABC-type protein transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{protein}_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{protein}_{[\text{side } 2]}$
Other name(s): PrtDEF (gene names); *hasDEF* (gene names); peptide-transporting ATPase (ambiguous)
Systematic name: ATP phosphohydrolase (ABC-type, peptide-exporting)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. This entry stands for a family of bacterial enzymes that are dedicated to the secretion of one or several closely related proteins belonging to the toxin, protease and lipase families. Examples from Gram-negative bacteria include α -hemolysin, cyclolysin, colicin V and siderophores, while examples from Gram-positive bacteria include bacteriocin, subtilin, competence factor and pediocin.
References: [143, 129, 34]

[EC 7.4.2.5 created 2000 as EC 3.6.3.43, transferred 2018 to EC 7.4.2.5, modified 2019]

EC 7.4.2.6

Accepted name: ABC-type oligopeptide transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{oligopeptide-}[\text{oligopeptide-binding protein}]_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{oligopeptide}_{[\text{side } 2]} + [\text{oligopeptide-binding protein}]_{[\text{side } 1]}$
Other name(s): oligopeptide permease; OppBCDF; oligopeptide ABC transporter; oligopeptide-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, oligopeptide-importing)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. Does not undergo phosphorylation during the transport process. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the import of oligopeptides of varying nature. The binding protein determines the specificity of the system. *cf.* EC 7.4.2.9, ABC-type dipeptide transporter.
References: [133, 213, 86, 191]

[EC 7.4.2.6 created 2000 as EC 3.6.3.23, transferred 2018 to EC 7.4.2.6]

EC 7.4.2.7

Accepted name: ABC-type α -factor-pheromone transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \alpha\text{-factor}_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \alpha\text{-factor}_{[\text{side } 2]}$
Other name(s): α -factor-transporting ATPase; α -factor-pheromone transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, α -factor-exporting)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. Does not undergo phosphorylation during the transport process. A yeast enzyme that exports the α -factor sex pheromone.
References: [169, 213]

[EC 7.4.2.7 created 2000 as EC 3.6.3.48, transferred 2018 to EC 7.4.2.7]

EC 7.4.2.8

Accepted name: protein-secreting ATPase
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{cellular protein}_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{cellular protein}_{[\text{side } 2]}$
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: [212, 166, 254, 11, 163, 218]

[EC 7.4.2.8 created 2000 as EC 3.6.3.50, transferred 2018 to EC 7.4.2.8]

EC 7.4.2.9

Accepted name: ABC-type dipeptide transporter

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{a dipeptide} \cdot [\text{dipeptide-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{a dipeptide}_{[\text{side 2}]} + [\text{dipeptide-binding protein}]_{[\text{side 1}]}$

Other name(s): dipeptide transporting ATPase; dipeptide ABC transporter; dppBCDF (gene names)

Systematic name: ATP phosphohydrolase (ABC-type, dipeptide-transporting)

Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the uptake of di- and tripeptides. The enzyme from *Pseudomonas aeruginosa* can interact with five different substrate binding proteins.

References: [1, 214, 145, 196]

[EC 7.4.2.9 created 2018]

EC 7.4.2.10

Accepted name: ABC-type glutathione transporter

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{glutathione} \cdot [\text{glutathione-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{glutathione}_{[\text{side 2}]} + [\text{glutathione-binding protein}]_{[\text{side 1}]}$

Other name(s): glutathione transporting ATPase; glutathione ABC transporter; *gsiACD* (gene names)

Systematic name: ATP phosphohydrolase (ABC-type, glutathione-importing)

Comments: A prokaryotic ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme from the bacterium *Escherichia coli* is a heterotrimeric complex that interacts with an extracytoplasmic substrate binding protein to mediate the uptake of glutathione.

References: [247, 175]

[EC 7.4.2.10 created 2019]

EC 7.4.2.11

Accepted name: ABC-type methionine transporter

Reaction: (1) $\text{ATP} + \text{H}_2\text{O} + \text{L-methionine} \cdot [\text{methionine-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{L-methionine}_{[\text{side 2}]} + [\text{methionine-binding protein}]_{[\text{side 1}]}$

(2) $\text{ATP} + \text{H}_2\text{O} + \text{D-methionine} \cdot [\text{methionine-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{D-methionine}_{[\text{side 2}]} + [\text{methionine-binding protein}]_{[\text{side 1}]}$

Other name(s): methionine transporting ATPase; methionine ABC transporter; *metNIQ* (gene names)

Systematic name: ATP phosphohydrolase (ABC-type, methionine-importing)

Comments: ABC-type (ATP-binding cassette-type) transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and functions to import methionine. The enzyme from *Escherichia coli* K-12 mediates the high affinity transport of both L- and D-methionine, as well as methionine-S-oxide and N-acetyl-DL-methionine.

References: [168, 287, 175]

[EC 7.4.2.11 created 2019]

EC 7.4.2.12

- Accepted name:** ABC-type cystine transporter
- Reaction:** (1) $\text{ATP} + \text{H}_2\text{O} + \text{L-cystine-}[\text{cystine-binding protein}]_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{L-cystine}_{[\text{side } 2]} + [\text{cystine-binding protein}]_{[\text{side } 1]}$
(2) $\text{ATP} + \text{H}_2\text{O} + \text{D-cystine-}[\text{cystine-binding protein}]_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{D-cystine}_{[\text{side } 2]} + [\text{cystine-binding protein}]_{[\text{side } 1]}$
- Other name(s):** cystine transporting ATPase; cystine ABC transporter
- Systematic name:** ATP phosphohydrolase (ABC-type, cystine-importing)
- Comments:** ABC-type (ATP-binding cassette-type) transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the high affinity import of trace cystine. The enzyme from *Escherichia coli* K-12 can import both isomers of cystine and a variety of related molecules including djenkolate, lanthionine, diaminopimelate and homocystine.
- References:** [29, 111]

[EC 7.4.2.12 created 2019]

EC 7.4.2.13

- Accepted name:** ABC-type tyrosine transporter
- Reaction:** $\text{ATP} + \text{H}_2\text{O} + \text{L-tyrosinyl-}[\text{tyrosine-binding protein}]_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{L-tyrosine}_{[\text{side } 2]} + [\text{tyrosine-binding protein}]_{[\text{side } 1]}$
- Systematic name:** ATP phosphohydrolase (ABC-type, L-tyrosine-importing)
- Comments:** An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme, found in Clostridioides, interacts with an extracytoplasmic substrate binding lipoprotein and mediates the import of L-tyrosine. L-phenylalanine is also transported however with lower efficiency.
- References:** [242]

[EC 7.4.2.13 created 2019]

EC 7.4.2.14

- Accepted name:** ABC-type antigen peptide transporter
- Reaction:** $\text{ATP} + \text{H}_2\text{O} + \text{antigen peptide}_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{antigen peptide}_{[\text{side } 2]}$
- Other name(s):** TAP1 (gene name); TAP2 (gene name)
- Systematic name:** ATP phosphohydrolase (ABC-type, antigen peptide-exporting)
- Comments:** An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. Does not undergo phosphorylation during the transport process. This entry describes vertebrate transporters involved in the transport of antigens from the cytoplasm to the endoplasmic reticulum for association with major histocompatibility complex (MHC) class I molecules. The substrates are generated mainly from degradation of cytosolic proteins by the proteasome.
- References:** [10, 173, 181]

[EC 7.4.2.14 created 2021]

EC 7.5 Catalysing the translocation of carbohydrates and their derivatives

Subclasses are based on the reaction processes that provide the driving force for the translocation. At present only one subclass is represented: EC 7.5.2 Translocation of carbohydrates and their derivatives linked to the hydrolysis of a nucleoside triphosphate.

EC 7.5.2 Linked to the hydrolysis of a nucleoside triphosphate

EC 7.5.2.1

- Accepted name:** ABC-type maltose transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{maltose-}[\text{maltose-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{maltose}_{[\text{side 2}]} + [\text{maltose-binding protein}]_{[\text{side 1}]}$
Other name(s): maltose ABC transporter; maltose-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, maltose-importing)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme, found in bacteria, interacts with an extracytoplasmic substrate binding protein and mediates the import of maltose and maltose oligosaccharides.
References: [99, 63, 133, 213, 86]

[EC 7.5.2.1 created 2000 as EC 3.6.3.19, transferred 2018 to EC 7.5.2.1]

EC 7.5.2.2

- Accepted name:** ABC-type oligosaccharide transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{oligosaccharide-}[\text{oligosaccharide-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{oligosaccharide}_{[\text{side 2}]} + [\text{oligosaccharide-binding protein}]_{[\text{side 1}]}$
Other name(s): oligosaccharide-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, oligosaccharide-importing)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme, found in bacteria, interacts with an extracytoplasmic substrate binding protein and mediates the import of lactose, melibiose and raffinose.
References: [99, 276, 201, 133, 213]

[EC 7.5.2.2 created 2000 as EC 3.6.3.18, transferred 2018 to EC 7.5.2.2]

EC 7.5.2.3

- Accepted name:** ABC-type β -glucan transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \beta\text{-glucan}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \beta\text{-glucan}_{[\text{side 2}]}$
Other name(s): β -glucan-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, β -glucan-exporting)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. An enzyme found in Gram-negative bacteria that exports β -glucans.
References: [74, 20, 213, 86]

[EC 7.5.2.3 created 2000 as EC 3.6.3.42, transferred 2018 to EC 7.5.2.3]

EC 7.5.2.4

- Accepted name:** ABC-type teichoic-acid transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{teichoic acid}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{teichoic acid}_{[\text{side 2}]}$
Other name(s): teichoic-acid-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, teichoic-acid-exporting)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. Does not undergo phosphorylation during the transport process. An enzyme found in Gram-positive bacteria that exports teichoic acid.
References: [74, 140, 190, 86]

[EC 7.5.2.4 created 2000 as EC 3.6.3.40, transferred 2018 to EC 7.5.2.4]

EC 7.5.2.5

Accepted name: ABC-type lipopolysaccharide transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{lipopolysaccharide}_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{lipopolysaccharide}_{[\text{side } 2]}$
Other name(s): *lptB* (gene name); lipopolysaccharide transport system; lipopolysaccharide-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, lipopolysaccharide-exporting)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. Does not undergo phosphorylation during the transport process. The enzyme, characterized from the bacterium *Escherichia coli*, functions as part of the lipopolysaccharide (LPS) export system, a seven protein system that translocates LPS from the inner- to the outer membrane. The ATPase activity in this system is implicated in releasing LPS from the inner membrane.
References: [239, 210, 180, 256, 186, 53]

[EC 7.5.2.5 created 2000 as EC 3.6.3.39, transferred 2018 to EC 7.5.2.5]

EC 7.5.2.6

Accepted name: ABC-type lipid A-core oligosaccharide transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{lipid A-core oligosaccharide}_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{lipid A-core oligosaccharide}_{[\text{side } 2]}$
Other name(s): MsbA; lipid flippase; ATP-dependent lipid A-core flippase
Systematic name: ATP phosphohydrolase (ABC-type, lipid A-core oligosaccharide-translocating)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme, best characterized from the bacterium *Escherichia coli*, is located in the inner membrane and mediates the movement of lipid A attached to the core oligosaccharide from the cytoplasm to the periplasmic side of the inner membrane, an important step in the lipopolysaccharide biosynthetic pathway. Not to be confused with EC 7.5.2.5, ABC-type lipopolysaccharide transporter (LptB), which is implicated in the translocation of LPS from the inner membrane to the outer membrane and acts later in the process.
References: [118, 289, 230]

[EC 7.5.2.6 created 2018]

EC 7.5.2.7

Accepted name: ABC-type D-ribose transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{D-ribose-}[\text{ribose-binding protein}]_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{D-ribose}_{[\text{side } 2]} + [\text{ribose-binding protein}]_{[\text{side } 1]}$
Other name(s): D-ribose transporting ATPase; D-ribose ABC transporter; *rhsACB* (gene names)
Systematic name: ATP phosphohydrolase (ABC-type, D-ribose-importing)
Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the high affinity uptake of D-ribose.
References: [22, 58]

[EC 7.5.2.7 created 2019]

EC 7.5.2.8

Accepted name: ABC-type D-allose transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{D-allose-}[\text{allose-binding protein}]_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{D-allose}_{[\text{side } 2]} + [\text{allose-binding protein}]_{[\text{side } 1]}$
Other name(s): D-allose transporting ATPase; D-allose ABC transporter; *alsBAC* (gene names)

Systematic name: ATP phosphohydrolase (ABC-type, D-allose-importing)
Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme from the bacterium *Escherichia coli* interacts with an extracytoplasmic substrate binding protein and mediates the high affinity uptake of D-allose, which can be used by the bacterium as a sole carbon source.
References: [127]

[EC 7.5.2.8 created 2019]

EC 7.5.2.9

Accepted name: ABC-type D-galactofuranose transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{D-galactofuranose-[galactofuranose-binding protein]}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{D-galactofuranose}_{[\text{side 2}]} + [\text{galactofuranose-binding protein}]_{[\text{side 1}]}$
Other name(s): D-galactofuranose transporting ATPase; D-galactofuranose ABC transporter
Systematic name: ATP phosphohydrolase (ABC-type, D-galactofuranose-transporting)
Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme from *Escherichia coli* interacts with a periplasmic substrate binding protein and mediates the high affinity uptake of D-galactofuranose. The periplasmic binding protein exhibits selective binding of D-galactofuranose over D-galactopyranose.
References: [106]

[EC 7.5.2.9 created 2019]

EC 7.5.2.10

Accepted name: ABC-type D-xylose transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{D-xylose-[xylose-binding protein]}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{D-xylose}_{[\text{side 2}]} + [\text{xylose-binding protein}]_{[\text{side 1}]}$
Other name(s): D-xylose transporting ATPase; D-xylose ABC transporter; *xyIFGH* (gene names)
Systematic name: ATP phosphohydrolase (ABC-type, D-xylose-transporting)
Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the high affinity uptake of D-xylose.
References: [238, 147]

[EC 7.5.2.10 created 2019]

EC 7.5.2.11

Accepted name: ABC-type D-galactose transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{D-galactose-[galactose-binding protein]}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{D-galactose}_{[\text{side 2}]} + [\text{galactose-binding protein}]_{[\text{side 1}]}$
Other name(s): D-galactose transporting ATPase; D-galactose ABC transporter; *mglBAC* (gene names)
Systematic name: ATP phosphohydrolase (ABC-type, D-galactose-importing)
Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. A bacterial enzyme, best characterized from *Escherichia coli* where it interacts with a periplasmic substrate binding protein and mediates the high affinity uptake of D-galactose and methyl- β -D-galactoside.
References: [104]

[EC 7.5.2.11 created 2019]

EC 7.5.2.12

- Accepted name:** ABC-type L-arabinose transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{L-arabinose-}[\text{arabinose-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{L-arabinose}_{[\text{side 2}]} + [\text{arabinose-binding protein}]_{[\text{side 1}]}$
Other name(s): L-arabinose transporting ATPase; L-arabinose ABC transporter; *araFGH* (gene names)
Systematic name: ATP phosphohydrolase (ABC-type, L-arabinose-importing)
Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the high-affinity uptake of L-arabinose.
References: [221, 105]

[EC 7.5.2.12 created 2019]

EC 7.5.2.13

- Accepted name:** ABC-type D-xylose/L-arabinose transporter
Reaction: (1) $\text{ATP} + \text{H}_2\text{O} + \text{D-xylose-}[\text{xylose-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{D-xylose}_{[\text{side 2}]} + [\text{xylose-binding protein}]_{[\text{side 1}]}$
(2) $\text{ATP} + \text{H}_2\text{O} + \text{L-arabinose-}[\text{arabinose-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{L-arabinose}_{[\text{side 2}]} + [\text{arabinose-binding protein}]_{[\text{side 1}]}$
Systematic name: ATP phosphohydrolase (ABC-type, D-xylose/L-arabinose-importing)
Comments: ATP-binding cassette (ABC) type transporter with a 10-transmembrane-spanning (TMD) subunit and a single nucleotide binding domain. The enzyme from the archaeon *Sulfolobus acidocaldarius* interacts with an extracytoplasmic sugar-binding protein and mediates the uptake of D-xylose and L-arabinose (*cf.* EC 7.5.2.10, ABC-type D-xylose transporter and EC 7.5.2.12, ABC-type L-arabinose transporter).
References: [265]

[EC 7.5.2.13 created 2019]

EC 7.6 Catalysing the translocation of other compounds

Subclasses are based on the reaction processes that provide the driving force for the translocation. At present only one subclass is represented: EC 7.6.2 Translocation of other compounds linked to the hydrolysis of a nucleoside triphosphate.

EC 7.6.2 Linked to the hydrolysis of a nucleoside triphosphate

EC 7.6.2.1

- Accepted name:** P-type phospholipid transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{phospholipid}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{phospholipid}_{[\text{side 2}]}$
Other name(s): Mg^{2+} -ATPase (ambiguous); flippase (ambiguous); aminophospholipid-transporting ATPase (ambiguous); phospholipid-translocating ATPase (ambiguous); phospholipid-transporting ATPase (ambiguous)
Systematic name: ATP phosphohydrolase (P-type, phospholipid-flipping)
Comments: A P-type ATPase that undergoes covalent phosphorylation during the transport cycle. Different forms of the enzyme move phospholipids such as phosphatidylcholine, lyso-phosphatidylcholine, phosphatidylserine, phosphatidylethanolamine, phosphatidylglycerol, sphingomyelin and glucosylceramide from one membrane face to the other ('flippase').
References: [174, 263, 246, 8, 4, 149, 115]

[EC 7.6.2.1 created 2000 as EC 3.6.3.1 (EC 3.6.3.13 created 2000, incorporated 2001), transferred 2018 to EC 7.6.2.1]

EC 7.6.2.2

- Accepted name:** ABC-type xenobiotic transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{xenobiotic}_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{xenobiotic}_{[\text{side } 2]}$
Other name(s): xenobiotic-transporting ATPase; multidrug-resistance protein; MDR protein; P-glycoprotein; pleiotropic-drug-resistance protein; PDR protein; steroid-transporting ATPase; ATP phosphohydrolase (steroid-exporting)
Systematic name: ATP phosphohydrolase (ABC-type, xenobiotic-exporting)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. Does not undergo phosphorylation during the transport process. The enzymes 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 also transport glutathione—drug conjugates (see EC 7.6.2.3, ABC-type glutathione-S-conjugate transporter) while others also show some ‘flippase’ activity (*cf.* EC 7.6.2.1, P-type phospholipid transporter).
References: [23, 77, 124, 148, 262, 86, 198, 177, 157]

[EC 7.6.2.2 created 2000 as EC 3.6.3.44 (EC 3.6.3.45 incorporated 2006), modified 2006, transferred 2018 to EC 7.6.2.2]

EC 7.6.2.3

- Accepted name:** ABC-type glutathione-S-conjugate transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{glutathione-S-conjugate}_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{glutathione-S-conjugate}_{[\text{side } 2]}$
Other name(s): multidrug resistance-associated protein 1; glutathione-S-conjugate-translocating ATPase; MRP; MRP1; ABCC1 (gene name); YBT1 (gene name); YCF1 (gene name)
Systematic name: ATP phosphohydrolase (ABC-type, glutathione-S-conjugate-exporting)
Comments: A eukaryotic ATP-binding cassette (ABC) type transporter that mediates the transport of glutathione-S-conjugates. The mammalian enzyme, which also transports some glucuronides, exports the substrates out of the cell, while plant and fungal transporters export them into the vacuole. Over-expression confers resistance to anticancer drugs by their efficient exportation in glutathione-S-conjugate form.
References: [285, 139, 146, 150, 60, 61]

[EC 7.6.2.3 created 2018]

EC 7.6.2.4

- Accepted name:** ABC-type fatty-acyl-CoA transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{fatty acyl CoA}_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{fatty acyl CoA}_{[\text{side } 2]}$
Other name(s): fatty-acyl-CoA-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, fatty-acyl-CoA-transporting)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. 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: [117, 98, 213]

[EC 7.6.2.4 created 2000 as EC 3.6.3.47, transferred 2018 to EC 7.6.2.4]

EC 7.6.2.5

- Accepted name:** ABC-type heme transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{heme}_{[\text{side } 1]} = \text{ADP} + \text{phosphate} + \text{heme}_{[\text{side } 2]}$
Other name(s): heme-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, heme-exporting)

Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. Does not undergo phosphorylation during the transport process. The enzyme has been described from Gram-negative bacteria and green plants.

References: [204, 114, 213]

[EC 7.6.2.5 created 2000 as EC 3.6.3.41, transferred 2018 to EC 7.6.2.5]

EC 7.6.2.6

Accepted name: ABC-type guanine transporter

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{guanine}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{guanine}_{[\text{side 2}]}$

Other name(s): guanine-transporting ATPase; white (gene name); brown (gene name)

Systematic name: ATP phosphohydrolase (ABC-type, guanine-importing)

Comments: An ATP-binding cassette (ABC) type transporter found in insects that transports guanine and other purines into pigment granules in the eye, where they are converted to pteridine pigments. The transporter is a heterodimer composed of two different peptides, each containing one membrane-spanning and one cytoplasmic ATP-binding domain. In *Drosophila*, this transporter is encoded by the white and brown genes.

References: [245, 68, 252, 86, 153]

[EC 7.6.2.6 created 2000 as EC 3.6.3.37, transferred 2018 to EC 7.6.2.6]

EC 7.6.2.7

Accepted name: ABC-type taurine transporter

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{taurine-}[\text{taurine-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{taurine}_{[\text{side 2}]} + [\text{taurine-binding protein}]_{[\text{side 1}]}$

Other name(s): *tauABC* (gene names); taurine ABC transporter; taurine-transporting ATPase

Systematic name: ATP phosphohydrolase (ABC-type, taurine-importing)

Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. Does not undergo phosphorylation during the transport process. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the high affinity uptake of taurine. In *Escherichia coli* the enzyme imports a range of sulfonates (including taurine) that can be used as a source of sulfur.

References: [261]

[EC 7.6.2.7 created 2000 as EC 3.6.3.36, transferred 2018 to EC 7.6.2.7]

EC 7.6.2.8

Accepted name: ABC-type vitamin B₁₂ transporter

Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{vitamin B}_{12}\text{-}[\text{cobalamin-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{vitamin B}_{12}_{[\text{side 2}]} + [\text{cobalamin-binding protein}]_{[\text{side 1}]}$

Other name(s): BtuCDF; vitamin B₁₂ ABC transporter; vitamin B₁₂-transporting ATPase

Systematic name: ATP phosphohydrolase (ABC-type, vitamin B₁₂-importing)

Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. Does not undergo phosphorylation during the transport process. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the high affinity uptake of cobalamin derivatives.

References: [76, 133, 213]

[EC 7.6.2.8 created 2000 as EC 3.6.3.33, transferred 2018 to EC 7.6.2.8]

EC 7.6.2.9

Accepted name: ABC-type quaternary amine transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{quaternary amine-}[\text{quaternary amine-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{quaternary amine}_{[\text{side 2}]} + [\text{quaternary amine-binding protein}]_{[\text{side 1}]}$
Other name(s): glycine betaine ABC transporter; ProVWX; quaternary-amine ABC transporter; quaternary-amine-transporting ATPase (ambiguous)
Systematic name: ATP phosphohydrolase (ABC-type, quaternary-amine-importing)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. Does not undergo phosphorylation during the transport process. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the high affinity uptake of quaternary amine derivatives.
References: [133, 123, 213]

[EC 7.6.2.9 created 2000 as EC 3.6.3.32, transferred 2018 to EC 7.6.2.9]

EC 7.6.2.10

Accepted name: ABC-type glycerol 3-phosphate transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \textit{sn}$ -glycerol 3-phosphate- $[\text{glycerol 3-phosphate-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \textit{sn}$ -glycerol 3-phosphate $_{[\text{side 2}]} + [\text{glycerol 3-phosphate-binding protein}]_{[\text{side 1}]}$
Other name(s): glycerol-3-phosphate ABC transporter; glycerol-3-phosphate-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, *sn*-glycerol 3-phosphate-importing)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. Does not undergo phosphorylation during the transport process. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the high affinity uptake of glycerol 3-phosphate and various glycerophosphodiester.
References: [213, 86, 9]

[EC 7.6.2.10 created 2000 as EC 3.6.3.20, transferred 2018 to EC 7.6.2.10]

EC 7.6.2.11

Accepted name: ABC-type polyamine transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{polyamine-}[\text{polyamine-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{polyamine}_{[\text{side 2}]} + [\text{polyamine-binding protein}]_{[\text{side 1}]}$
Other name(s): polyamine ABC transporter; polyamine-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, polyamine-importing)
Comments: An ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. Does not undergo phosphorylation during the transport process. A bacterial enzyme that imports putrescine and spermidine. In *Escherichia coli* the enzyme imports spermidine preferentially.
References: [119, 133, 213]

[EC 7.6.2.11 created 2000 as EC 3.6.3.31, transferred 2018 to EC 7.6.2.11]

EC 7.6.2.12

Accepted name: ABC-type capsular-polysaccharide transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{capsular polysaccharide-}[\text{capsular polysaccharide-binding protein}]_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{capsular polysaccharide}_{[\text{side 2}]} + [\text{capsular polysaccharide-binding protein}]_{[\text{side 1}]}$
Other name(s): capsular-polysaccharide-transporting ATPase
Systematic name: ATP phosphohydrolase (ABC-type, capsular-polysaccharide-exporting)
Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains. Does not undergo phosphorylation during the transport process. An enzyme that exports capsular polysaccharide in Gram-negative bacteria.
References: [74, 190, 194, 213, 86]

[EC 7.6.2.12 created 2000 as EC 3.6.3.38, transferred 2018 to EC 7.6.2.12]

EC 7.6.2.13

Accepted name: ABC-type autoinducer-2 transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + (2R,4S)\text{-2-methyl-2,3,3,4-tetrahydroxytetrahydrofuran-[AI-2-binding protein]}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + (2R,4S)\text{-2-methyl-2,3,3,4-tetrahydroxytetrahydrofuran}_{[\text{side 2}]} + [\text{AI-2-binding protein}]_{[\text{side 1}]}$
Other name(s): autoinducer-2 transporting ATPase; autoinducer-2 ABC transporter; LsrACDB (gene names)
Systematic name: ATP phosphohydrolase (ABC-type, AI-2 importing)
Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. A bacterial enzyme that interacts with an extracytoplasmic substrate binding protein and mediates the uptake of the signalling molecule (2R,4S)-2-methyl-2,3,3,4-tetrahydroxytetrahydrofuran (also known as autoinducer-2).
References: [249, 278]

[EC 7.6.2.13 created 2019]

EC 7.6.2.14

Accepted name: ABC-type aliphatic sulfonate transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{aliphatic sulfonate-[sulfonate-binding protein]}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{aliphatic sulfonate}_{[\text{side 2}]} + [\text{sulfonate-binding protein}]_{[\text{side 1}]}$
Other name(s): aliphatic sulfonate transporting ATPase; alkane sulfonate ABC transporter; aliphatic sulfonate ABC transporter; *ssuACB* (gene names)
Systematic name: ATP phosphohydrolase (ABC-type, aliphatic sulfonate-importing)
Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme from the bacterium *Escherichia coli* K-12 interacts with an extracytoplasmic substrate binding protein and imports a broad range of aliphatic sulfonates for use as a source of sulfur.
References: [260, 125, 64]

[EC 7.6.2.14 created 2019]

EC 7.6.2.15

Accepted name: ABC-type thiamine transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{thiamine-[thiamine-binding protein]}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{thiamine}_{[\text{side 2}]} + [\text{thiamine-binding protein}]_{[\text{side 1}]}$
Other name(s): thiamin transporting ATPase; thiamine ABC transporter; thiamin ABC transporter; thiamine transporting ATPase; *thiBPQ* (gene names)
Systematic name: ATP phosphohydrolase (ABC-type, thiamine-importing)
Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme, characterized from the bacterium *Salmonella typhimurium*, is a heterodimeric complex that interacts with an extracytoplasmic substrate binding protein and functions to import thiamine, thiamine monophosphate and thiamine diphosphate.
References: [271]

[EC 7.6.2.15 created 2019]

EC 7.6.2.16

Accepted name: ABC-type putrescine transporter
Reaction: $\text{ATP} + \text{H}_2\text{O} + \text{putrescine-[putrescine-binding protein]}_{[\text{side 1}]} = \text{ADP} + \text{phosphate} + \text{putrescine}_{[\text{side 2}]} + [\text{putrescine-binding protein}]_{[\text{side 1}]}$
Other name(s): putrescine transporting ATPase; putrescine ABC transporter; potFGHI (gene names)

Systematic name: ATP phosphohydrolase (ABC-type, putrescine-importing)

Comments: ATP-binding cassette (ABC) type transporter, characterized by the presence of two similar ATP-binding domains/proteins and two integral membrane domains/proteins. The enzyme from the bacterium *Escherichia coli* interacts with an extracytoplasmic substrate binding protein and mediates the high affinity uptake of putrescine. Differs in specificity from EC 7.6.2.11, ABC-type polyamine transporter.

References: [195, 253]

[EC 7.6.2.16 created 2019]

References

- [1] W.N. Abouhamad, M. Manson, M.M. Gibson, and C.F. Higgins. Peptide transport and chemotaxis in *Escherichia coli* and *Salmonella typhimurium*: characterization of the dipeptide permease (Dpp) and the dipeptide-binding protein. *Mol. Microbiol.*, 5:1035–1047, 1991.
- [2] J.P. Abrahams, A.G.W. Leslie, R. Lutter, and J.F. Walker. Structure at 2.8 Å resolution of F₁-ATPase from bovine heart mitochondria. *Nature*, 375:621–628, 1994.
- [3] J. Abramson, S. Riistama, G. Larsson, A. Jasaitis, M. Svensson-Ek, L. Laakkonen, A. Puustinen, S. Iwata, and M. Wikstrom. The structure of the ubiquinol oxidase from *Escherichia coli* and its ubiquinone binding site. *Nat. Struct. Biol.*, 7:910–917, 2000.
- [4] N. Alder-Baerens, Q. Lisman, L. Luong, T. Pomorski, and J.C. Holthuis. Loss of P4 ATPases Drs2p and Dnf3p disrupts aminophospholipid transport and asymmetry in yeast post-Golgi secretory vesicles. *Mol. Biol. Cell*, 17:1632–1642, 2006.
- [5] J.L. Andersen, P. Gourdon, J.V. Moller, J.P. Morth, and P. Nissen. Crystallization and preliminary structural analysis of the *Listeria monocytogenes* Ca(2+)-ATPase LMCA₁. *Acta Crystallogr. Sect. F Struct. Biol. Cryst. Commun.*, 67:718–722, 2011.
- [6] A. Angerer, B. Klupp, and V. Braun. Iron transport systems of *Serratia marcescens*. *J. Bacteriol.*, 174:1378–1387, 1992.
- [7] A.A. Arteni, P. Zhang, N. Battchikova, T. Ogawa, E.M. Aro, and E.J. Boekema. Structural characterization of NDH-1 complexes of *Thermosynechococcus elongatus* by single particle electron microscopy. *Biochim. Biophys. Acta*, 1757:1469–1475, 2006.
- [8] M.E. Auland, B.D. Roufogalis, P.F. Devaux, and A. Zachowski. Reconstitution of ATP-dependent aminophospholipid translocation in proteoliposomes. *Proc. Natl. Acad. Sci. USA*, 91:10938–10942, 1994.
- [9] H. Bahl, G. Burchhardt, and A. Wienecke. Nucleotide sequence of two *Clostridium thermosulfurogenes* EM1 genes homologous to *Escherichia coli* genes encoding integral membrane components of binding-protein-dependent transport systems. *FEMS Microbiol. Lett.*, 65:83–87, 1991.
- [10] S. Bahram, D. Arnold, M. Bresnahan, J.L. Strominger, and T. Spies. Two putative subunits of a peptide pump encoded in the human major histocompatibility complex class II region. *Proc. Natl. Acad. Sci. USA*, 88:10094–10098, 1991.
- [11] B. Baker, P. Zambryski, B. Staskawicz, and S.P. Dinesh-Kumar. Signaling in plant-microbe interactions. *Science*, 276:726–733, 1997.
- [12] L. Banci, I. Bertini, S. Ciofi-Baffoni, M. D’Onofrio, L. Gonnelli, F.C. Marhuenda-Egea, and F.J. Ruiz-Duenas. Solution structure of the N-terminal domain of a potential copper-translocating P-type ATPase from *Bacillus subtilis* in the apo and Cu(I) loaded states. *J. Mol. Biol.*, 317:415–429, 2002.
- [13] T.M. Bandejas, M.M. Pereira, M. Teixeira, P. Moenne-Loccoz, and N.J. Blackburn. Structure and coordination of CuB in the *Acidianus ambivalens* aa₃ quinol oxidase heme-copper center. *J. Biol. Inorg. Chem.*, 10:625–635, 2005.
- [14] S. Banerjee, S. Paul, L.T. Nguyen, B.C. Chu, and H.J. Vogel. FecB, a periplasmic ferric-citrate transporter from *E. coli*, can bind different forms of ferric-citrate as well as a wide variety of metal-free and metal-loaded tricarboxylic acids. *Metallomics*, 8:125–133, 2016.
- [15] B. Barquera, P. Hellwig, W. Zhou, J.E. Morgan, C.C. Hase, K.K. Gosink, M. Nilges, P.J. Bruesehoff, A. Roth, C.R. Lancaster, and R.B. Gennis. Purification and characterization of the recombinant Na⁺-translocating NADH:quinone oxidoreductase from *Vibrio cholerae*. *Biochemistry*, 41:3781–3789, 2002.
- [16] B. Barquera, M.J. Nilges, J.E. Morgan, L. Ramirez-Silva, W. Zhou, and R.B. Gennis. Mutagenesis study of the 2Fe-2S center and the FAD binding site of the Na⁺-translocating NADH:ubiquinone oxidoreductase from *Vibrio cholerae*. *Biochemistry*, 43:12322–12330, 2004.
- [17] N. Battchikova, L. Wei, L. Du, L. Bersanini, E.M. Aro, and W. Ma. Identification of novel Ssl0352 protein (NdhS), essential for efficient operation of cyclic electron transport around photosystem I, in NADPH:plastoquinone oxidoreductase (NDH-1) complexes of *Synechocystis* sp. PCC 6803. *J. Biol. Chem.*, 286:36992–37001, 2011.

- [18] S.J. Beard, R. Hashim, J. Membrillo-Hernández, M.N. Hughes, and R.K. Poole. Zinc(II) tolerance in *Escherichia coli* K-12: evidence that the *zntA* gene (*o732*) encodes a cation transport ATPase. *Mol. Microbiol.*, 25:883–891, 1997.
- [19] P. Beattie, K. Tan, R.M. Bourne, D. Leach, P.R. Rich, and F.B. Ward. Cloning and sequencing of four structural genes for the Na⁺-translocating NADH-ubiquinone oxidoreductase of *Vibrio alginolyticus*. *FEBS Lett.*, 356:333–338, 1994.
- [20] A. Becker, H. Kuster, K. Niehaus, and A. Puhler. Extension of the *Rhizobium meliloti* succinoglycan biosynthesis gene cluster: identification of the *exsA* gene encoding an ABC transporter protein, and the *exsB* gene which probably codes for a regulator of succinoglycan biosynthesis. *Mol. Gen. Genet.*, 249:487–497, 1995.
- [21] I. Belevich, V.B. Borisov, J. Zhang, K. Yang, A.A. Konstantinov, R.B. Gennis, and M.I. Verkhovsky. Time-resolved electrometric and optical studies on cytochrome *bd* suggest a mechanism of electron-proton coupling in the di-heme active site. *Proc. Natl. Acad. Sci. USA*, 102:3657–3662, 2005.
- [22] A.W. Bell, S.D. Buckel, J.M. Groarke, J.N. Hope, D.H. Kingsley, and M.A. Hermodson. The nucleotide sequences of the *rbsD*, *rbsA*, and *rbsC* genes of *Escherichia coli* K12. *J. Biol. Chem.*, 261:7652–7658, 1986.
- [23] W.T. Bellamy. P-glycoproteins and multidrug resistance. *Annu. Rev. Pharmacol. Toxicol.*, 36:161–183, 1996.
- [24] G.A. Belogurov, A.M. Malinen, M.V. Turkina, U. Jalonen, K. Ryttonen, A.A. Baykov, and R. Lahti. Membrane-bound pyrophosphatase of *Thermotoga maritima* requires sodium for activity. *Biochemistry*, 44:2088–2096, 2005.
- [25] B. Benito, F.J. Quintero, and A. Rodriguez-Navarro. Overexpression of the sodium ATPase of *Saccharomyces cerevisiae*: conditions for phosphorylation from ATP and P_i. *Biochim. Biophys. Acta*, 1328:214–226, 1997.
- [26] A. Berczi, D. Su, and H. Asard. An *Arabidopsis* cytochrome *b₅₆₁* with *trans*-membrane ferrireductase capability. *FEBS Lett.*, 581:1505–1508, 2007.
- [27] M. Berg, H. Hilbi, and P. Dimroth. The acyl carrier protein of malonate decarboxylase of *Malonomonas rubra* contains 2'-(5''-phosphoribosyl)-3'-dephosphocoenzyme A as a prosthetic group. *Biochemistry*, 35:4689–4696, 1996.
- [28] M. Berg, H. Hilbi, and P. Dimroth. Sequence of a gene cluster from *Malonomonas rubra* encoding components of the malonate decarboxylase Na⁺ pump and evidence for their function. *Eur. J. Biochem.*, 245:103–115, 1997.
- [29] E.A. Berger and L.A. Heppel. A binding protein involved in the transport of cystine and diaminopimelic acid in *Escherichia coli*. *J. Biol. Chem.*, 247:7684–7694, 1972.
- [30] J. Berthold, M.F. Bauer, H.C. Schneider, C. Klaus, K. Dietmeier, W. Neupert, and M. Brunner. The MIM complex mediates preprotein translocation across the mitochondrial inner membrane and couples it to the mt-Hsp70/ATP-driving system. *Cell*, 81:1085–1093, 1995.
- [31] L.E. Bevers, P.L. Hagedoorn, G.C. Krijger, and W.R. Hagen. Tungsten transport protein A (WtpA) in *Pyrococcus furiosus*: the first member of a new class of tungstate and molybdate transporters. *J. Bacteriol.*, 188:6498–6505, 2006.
- [32] E. Biegel and V. Muller. Bacterial Na⁺-translocating ferredoxin:NAD⁺ oxidoreductase. *Proc. Natl. Acad. Sci. USA*, 107:18138–18142, 2010.
- [33] E. Biegel, S. Schmidt, and V. Muller. Genetic, immunological and biochemical evidence for a Rnf complex in the acetogen *Acetobacterium woodii*. *Environ. Microbiol.*, 11:1438–1443, 2009.
- [34] R. Binet, S. Létoffé, J.M. Ghigo, P. Delepaire, and C. Wanderman. Protein secretion by Gram-negative bacterial ABC exporters - a review. *Gene*, 192:7–11, 1997.
- [35] T. Bizouarn, O. Fjellstrom, J. Meuller, M. Axelsson, A. Bergkvist, C. Johansson, B. Goran Karlsson, and J. Rydstrom. Proton translocating nicotinamide nucleotide transhydrogenase from *E. coli*. Mechanism of action deduced from its structural and catalytic properties. *Biochim. Biophys. Acta*, 1457:211–228, 2000.
- [36] A. Blair, L. Ngo, J. Park, I.T., Saier Paulsen, , and Jr. Phylogenetic analyses of the homologous transmembrane channel-forming proteins of the F_oF₁-ATPases of bacteria, chloroplasts and mitochondria. *Microbiology*, 142:17–32, 1996.
- [37] A.V. Bogachev, Y.V. Bertsova, B. Barquera, and M.I. Verkhovsky. Sodium-dependent steps in the redox reactions of the Na⁺-motive NADH:quinone oxidoreductase from *Vibrio Harveyi*. *Biochemistry*, 40:7318–7323, 2001.

- [38] U. Bomer, M. Meijer, A.C. Maarse, A. Honlinger, P.J. Dekker, N. Pfanner, and J. Rassow. Multiple interactions of components mediating preprotein translocation across the inner mitochondrial membrane. *EMBO J.*, 16:2205–2216, 1997.
- [39] V.B. Borisov, R.B. Gennis, J. Hemp, and M.I. Verkhovskiy. The cytochrome *bd* respiratory oxygen reductases. *Biochim. Biophys. Acta*, 1807:1398–1413, 2011.
- [40] V.B. Borisov, R. Murali, M.L. Verkhovskaya, D.A. Bloch, H. Han, R.B. Gennis, and M.I. Verkhovskiy. Aerobic respiratory chain of *Escherichia coli* is not allowed to work in fully uncoupled mode. *Proc. Natl. Acad. Sci. USA*, 108:17320–17324, 2011.
- [41] M. Bott, K. Pfister, P. Burda, O. Kalbermatter, G. Woehlke, and P. Dimroth. Methylmalonyl-CoA decarboxylase from *Propionigenium modestum* – cloning and sequencing of the structural genes and purification of the enzyme complex. *Eur. J. Biochem.*, 250:590–599, 1997.
- [42] P.D. Boyer. The binding change mechanism for ATP synthase - some probabilities and possibilities. *Biochim. Biophys. Acta*, 1140:215–250, 1993.
- [43] M. Braibant, P. LeFevre, L. de Wit, J. Ooms, P. Peirs, K. Huygen, R. Wattiez, and J. Content. Identification of a second *Mycobacterium tuberculosis* gene cluster encoding proteins of an ABC phosphate transporter. *FEBS Lett.*, 394:206–212, 1996.
- [44] D.F. Bruhn, J. Li, S. Silver, F. Roberto, and B.P. Rosen. The arsenical resistance operon of IncN plasmid R46. *FEMS Microbiol. Lett.*, 139:149–153, 1996.
- [45] W. Buckel. Sodium ion-translocating decarboxylases. *Biochim. Biophys. Acta*, 1505:15–27, 2001.
- [46] W.S. Buckel and R. Semmler. Purification, characterisation and reconstitution of glutaconyl-CoA decarboxylase, a biotin-dependent sodium pump from anaerobic bacteria. *Eur. J. Biochem.*, 136:427–434, 1983.
- [47] N.R. Bury, M. Grosell, A.K. Grover, and C.M. Wood. ATP-dependent silver transport across the basolateral membrane of rainbow trout gills. *Toxicol. Appl. Pharmacol.*, 159:1–8, 1999.
- [48] E. Carafoli. The Ca²⁺ pump of the plasma membrane. *J. Biol. Chem.*, 267:2115–2118, 1992.
- [49] J.P. Castillo, H. Rui, D. Basilio, A. Das, B. Roux, R. Latorre, F. Bezanilla, and M. Holmgren. Mechanism of potassium ion uptake by the Na⁺/K⁺-ATPase. *Nat. Commun.*, 6:7622–7622, 2015.
- [50] P. Catty, A. de Kerchove d’Exaerde, and A. Goffeau. The complete inventory of the yeast *Saccharomyces cerevisiae* P-type transport ATPases. *FEBS Lett.*, 409:325–332, 1997.
- [51] S.S. Chenault and C.F. Earhart. Organization of genes encoding membrane proteins of the *Escherichia coli* ferrienterobactin permease. *Mol. Microbiol.*, 5:1405–1413, 1991.
- [52] J. Cheng, A.A. Guffanti, and T.A. Krulwich. A two-gene ABC-type transport system that extrudes Na⁺ in *Bacillus subtilis* is induced by ethanol or protonophore. *Mol. Microbiol.*, 23:1107–1120, 1997.
- [53] S.S. Chng, L.S. Gronenberg, and D. Kahne. Proteins required for lipopolysaccharide assembly in *Escherichia coli* form a transenvelope complex. *Biochemistry*, 49:4565–4567, 2010.
- [54] S.K. Choi, M.T. Lin, H. Ouyang, and R.B. Gennis. Searching for the low affinity ubiquinone binding site in cytochrome *bo*₃ from *Escherichia coli*. *Biochim Biophys Acta Bioenerg*, 1858:366–370, 2017.
- [55] S.K. Choi, L. Schurig-Briccio, Z. Ding, S. Hong, C. Sun, and R.B. Gennis. Location of the Substrate Binding Site of the Cytochrome *bo*₃ Ubiquinol Oxidase from *Escherichia coli*. *J. Am. Chem. Soc.*, 139:8346–8354, 2017.
- [56] D.M. Clarke and P.D. Bragg. Cloning and expression of the transhydrogenase gene of *Escherichia coli*. *J. Bacteriol.*, 162:367–373, 1985.
- [57] D.M. Clarke and P.D. Bragg. Purification and properties of reconstitutively active nicotinamide nucleotide transhydrogenase of *Escherichia coli*. *Eur. J. Biochem.*, 149:517–523, 1985.
- [58] M.C. Clifton, M.J. Simon, S.K. Erramilli, H. Zhang, J. Zaitseva, M.A. Hermodson, and C.V. Stauffacher. *In vitro* re-assembly of the ribose ATP-binding cassette transporter reveals a distinct set of transport complexes. *J. Biol. Chem.*, 290:5555–5565, 2015.

- [59] K. Cline, N.F. Ettinger, and S.M. Theg. Protein-specific energy requirements for protein transport across or into thylakoid membranes. Two luminal proteins are transported in the absence of ATP. *J. Biol. Chem.*, 267:2688–2696, 1992.
- [60] S.P. Cole. Multidrug resistance protein 1 (MRP1, ABCC1), a "multitasking" ATP-binding cassette (ABC) transporter. *J. Biol. Chem.*, 289:30880–30888, 2014.
- [61] A.G. Cordente, D.L. Capone, and C.D. Curtin. Unravelling glutathione conjugate catabolism in *Saccharomyces cerevisiae*: the role of glutathione/dipeptide transporters and vacuolar function in the release of volatile sulfur compounds 3-mercaptohexan-1-ol and 4-mercapto-4-methylpentan-2-one. *Appl. Microbiol. Biotechnol.*, 99:9709–9722, 2015.
- [62] W.A. Cramer and H. Zhang. Consequences of the structure of the cytochrome *b₆f* complex for its charge transfer pathways. *Biochim. Biophys. Acta*, 1757:339–345, 2006.
- [63] E. Dassa and S. Muir. Membrane topology of MalG, an inner membrane protein from the maltose transport system of *Escherichia coli*. *Mol. Microbiol.*, 7:29–38, 1993.
- [64] A.L. Davidson, E. Dassa, C. Orelle, and J. Chen. Structure, function, and evolution of bacterial ATP-binding cassette systems. *Microbiol. Mol. Biol. Rev.*, 72:317–364, 2008.
- [65] P. Dimroth. Characterization of a membrane-bound biotin-containing enzyme: oxaloacetate decarboxylase from *Klebsiella aerogenes*. *Eur. J. Biochem.*, 115:353–358, 1981.
- [66] P. Dimroth. The role of biotin and sodium in the decarboxylation of oxaloacetate by the membrane-bound oxaloacetate decarboxylase from *Klebsiella aerogenes*. *Eur. J. Biochem.*, 121:435–441, 1982.
- [67] P. Dimroth and H. Hilbi. Enzymic and genetic basis for bacterial growth on malonate. *Mol. Microbiol.*, 25:3–10, 1997.
- [68] T.D. Dreesen, D.H. Johnson, and S. Henikoff. The brown protein of *Drosophila melanogaster* is similar to the white protein and to components of active transport complexes. *Mol. Cell Biol.*, 8:5206–5215, 1988.
- [69] A.L. Ducluzeau, S. Ouchane, and W. Nitschke. The *cbb3* oxidases are an ancient innovation of the domain bacteria. *Mol. Biol. Evol.*, 25:1158–1166, 2008.
- [70] R.G. Efremov, R. Baradaran, and L.A. Sazanov. The architecture of respiratory complex I. *Nature*, 465:441–445, 2010.
- [71] A. Elbehti, W. Nitschke, P. Tron, C. Michel, and D. Lemesle-Meunier. Redox components of cytochrome *bc*-type enzymes in acidophilic prokaryotes. I. Characterization of the cytochrome *bc₁*-type complex of the acidophilic ferrous ion-oxidizing bacterium *Thiobacillus ferrooxidans*. *J. Biol. Chem.*, 274:16760–16765, 1999.
- [72] E. Eren and J.M. Argüello. *Arabidopsis* HMA2, a divalent heavy metal-transporting P(1B)-type ATPase, is involved in cytoplasmic Zn²⁺ homeostasis. *Plant Physiol.*, 136:3712–3723, 2004.
- [73] B. Fan and B.P. Rosen. Biochemical characterization of CopA, the *Escherichia coli* Cu(I)-translocating P-type ATPase. *J. Biol. Chem.*, 277:46987–46992, 2002.
- [74] M.J. Fath and R. Kolter. ABC transporters: bacterial exporters. *Microbiol. Rev.*, 57:995–1017, 1993.
- [75] T. Flatmark and O. Terland. Cytochrome *b₅₆₁* of the bovine adrenal chromaffin granules. A high potential *b*-type cytochrome. *Biochim. Biophys. Acta*, 253:487–491, 1971.
- [76] M.J. Friedrich, L.C. de Veaux, and R.J. Kadner. Nucleotide sequence of the *btuCED* genes involved in vitamin B₁₂ transport in *Escherichia coli* and homology with components of periplasmic-binding-protein-dependent transport systems. *J. Bacteriol.*, 167:928–934, 1986.
- [77] C.M. Frijters, R. Ottenhoff, M.J. Van Wijland, C. Van Nieuwkerk, A.K. Groen, and R.P. Oude-Elferink. Influence of bile salts on hepatic *mdr2* P-glycoprotein expression. *Adv. Enzyme Regul.*, 36:351–363, 1996.
- [78] J.H. Galivan and S.H.G. Allen. Methylmalonyl coenzyme A decarboxylase. Its role in succinate decarboxylation by *Micrococcus lactilyticus*. *J. Biol. Chem.*, 243:1253–1261, 1968.
- [79] M. Gassel, A. Siebers, W. Epstein, and K. Altendorf. Assembly of the Kdp complex, the multi-subunit K⁺-transport ATPase of *Escherichia coli*. *Biochim. Biophys. Acta*, 1415:77–84, 1998.

- [80] G. Gilderson, A. Aagaard, C.M. Gomes, P. Adelroth, M. Teixeira, and P. Brzezinski. Kinetics of electron and proton transfer during O₂ reduction in cytochrome *aa*₃ from *A. ambivalens*: an enzyme lacking Glu(I-286). *Biochim. Biophys. Acta*, 1503:261–270, 2001.
- [81] A. Glanfield, D.P. McManus, D.J. Smyth, E.M. Lovas, A. Loukas, G.N. Gobert, and M.K. Jones. A cytochrome *b*₅₆₁ with ferric reductase activity from the parasitic blood fluke, *Schistosoma japonicum*. *PLoS Negl. Trop. Dis.*, 4:e884–e884, 2010.
- [82] N.A. Glavas, C. Hou, and P.D. Bragg. Involvement of histidine-91 of the β subunit in proton translocation by the pyridine nucleotide transhydrogenase of *Escherichia coli*. *Biochemistry*, 34:7694–7702, 1995.
- [83] M. Gleissner, U. Kaiser, E. Antonopoulos, and G. Schafer. The archaeal SoxABCD complex is a proton pump in *Sulfolobus acidocaldarius*. *J. Biol. Chem.*, 272:8417–8426, 1997.
- [84] A. Goffeau and C. Slayman. The proton-translocating ATPase of the fungal plasma membrane. *Biochim. Biophys. Acta*, 639:197–223, 1981.
- [85] M. Gonzalez-Guerrero and J.M. Arguello. Mechanism of Cu⁺-transporting ATPases: soluble Cu⁺ chaperones directly transfer Cu⁺ to transmembrane transport sites. *Proc. Natl. Acad. Sci. USA*, 105:5992–5997, 2008.
- [86] J.K. Griffiths and C.E. Sansom. In *The Transporter Factsbook*. Academic Press, San Diego, 1998.
- [87] A.M. Grunden and K.T. Shanmugam. Molybdate transport and regulation in bacteria. *Arch. Mikrobiol.*, 168:345–354, 1997.
- [88] H.H. Guan, Y.C. Hsieh, P.J. Lin, Y.C. Huang, M. Yoshimura, L.Y. Chen, S.K. Chen, P. Chuankhayan, C.C. Lin, N.C. Chen, A. Nakagawa, S.I. Chan, and C.J. Chen. Structural insights into the electron/proton transfer pathways in the quinol:fumarate reductase from *Desulfovibrio gigas*. *Sci. Rep.*, 8:14935–14935, 2018.
- [89] A. Gupta, K. Matsui, J.F. Lo, and S. Silver. Molecular basis for resistance to silver cations in *Salmonella*. *Nature Med.*, 5:183–188, 1999.
- [90] K. Hantke. Bacterial zinc uptake and regulators. *Curr. Opin. Microbiol.*, 8:196–202, 2005.
- [91] Y. Hatefi, C.I. Ragan, and Y.M. Galante. The enzymes and the enzyme complexes of the mitochondrial oxidative phosphorylation system. In A. Martonosi, editor, *The Enzymes of Biological Membranes*, volume 4, pages 1–70. Plenum Press, New York, 2nd edition, 1985.
- [92] R. Hedrich, A. Kurkdjian, J. Guern, and U.I. Flugge. Comparative studies on the electrical properties of the H⁺ translocating ATPase and pyrophosphatase of the vacuolar-lysosomal compartment. *EMBO J.*, 8:2835–2841, 1989.
- [93] J.K. Hendricks and H.L. Mobley. *Helicobacter pylori* ABC transporter: effect of allelic exchange mutagenesis on urease activity. *J. Bacteriol.*, 179:5892–5902, 1997.
- [94] W. Henning, L. Vo, J. Albanese, and B.C. Hill. High-yield purification of cytochrome *aa*₃ and cytochrome *caa*₃ oxidases from *Bacillus subtilis* plasma membranes. *Biochem. J.*, 309:279–283, 1995.
- [95] S.J. Hersey, A. Matheravidathu Perez, Sachs S., and G. Gastric H⁺-K⁺-ATPase in situ: evidence for compartmentalization. *Am. J. Physiol.*, 257:G539–G547, 1989.
- [96] S.M. Herter, C.M. Kortluke, and G. Drews. Complex I of *Rhodobacter capsulatus* and its role in reverted electron transport. *Arch. Microbiol.*, 169:98–105, 1998.
- [97] V. Hess, K. Schuchmann, and V. Muller. The ferredoxin:NAD⁺ oxidoreductase (Rnf) from the acetogen *Acetobacterium woodii* requires Na⁺ and is reversibly coupled to the membrane potential. *J. Biol. Chem.*, 288:31496–31502, 2013.
- [98] E.H. Hettema, C.W.T. van Roermund, , and B. , van den Berg. M., Vilela, C., Rodrigues-Posada, C., Wanders, R.J.A. and Tabak, H.F. The ABC transporter proteins Pat1 and Pat2 are required for import of long-chain fatty acids into peroxisomes of *Saccharomyces cerevisiae*. *EMBO J.*, 15:3813–3822, 1996.
- [99] C.F. Higgins. ABC transporters: from microorganisms to man. *Annu. Rev. Cell Biol.*, 8:67–113, 1992.
- [100] H. Hilbi, I. Dehning, B. Schink, and P. Dimroth. Malonate decarboxylase of *Malonomonas rubra*, a novel type of biotin-containing acetyl enzyme. *Eur. J. Biochem.*, 207:117–123, 1992.

- [101] H. Hilbi and P. Dimroth. Purification and characterization of a cytoplasmic enzyme component of the Na⁺-activated malonate decarboxylase system of *Malonomonas rubra*: acetyl-S-acyl carrier protein: malonate acyl carrier protein-SH transferase. *Arch. Microbiol.*, 162:48–56, 1994.
- [102] W. Hilpert and P. Dimroth. Conversion of the chemical energy of methylmalonyl-CoA decarboxylation into a Na⁺ gradient. *Nature*, 296:584–585, 1982.
- [103] A. Hoffmann, W. Hilpert, and P. Dimroth. The carboxyltransferase activity of the sodium-ion-translocating methylmalonyl-CoA decarboxylase of *Veillonella alcalescens*. *Eur. J. Biochem.*, 179:645–650, 1989.
- [104] R.W. Hogg, C. Voelker, and I. Von Carlowitz. Nucleotide sequence and analysis of the *mgl* operon of *Escherichia coli* K12. *Mol. Gen. Genet.*, 229:453–459, 1991.
- [105] B.F. Horazdovsky and R.W. Hogg. Genetic reconstitution of the high-affinity L-arabinose transport system. *J. Bacteriol.*, 171:3053–3059, 1989.
- [106] R.S. Horler, A. Muller, D.C. Williamson, J.R. Potts, K.S. Wilson, and G.H. Thomas. Furanose-specific sugar transport: characterization of a bacterial galactofuranose-binding protein. *J. Biol. Chem.*, 284:31156–31163, 2009.
- [107] C.S. Huang, B.P. Pedersen, and D.L. Stokes. Crystal structure of the potassium-importing KdpFABC membrane complex. *Nature*, 546:681–685, 2017.
- [108] J.B. Huder and P. Dimroth. Expression of the sodium ion pump methylmalonyl-coenzyme A-decarboxylase from *Veillonella parvula* and of mutated enzyme specimens in *Escherichia coli*. *J. Bacteriol.*, 177:3623–3630, 1995.
- [109] C. Hunte, V. Zickermann, and U. Brandt. Functional modules and structural basis of conformational coupling in mitochondrial complex I. *Science*, 329:448–451, 2010.
- [110] E. Hurt and G. Hauska. A cytochrome *flb*₆ complex of five polypeptides with plastoquinol-plastocyanin-oxidoreductase activity from spinach chloroplasts. *Eur. J. Biochem.*, 117:591–595, 1981.
- [111] K.R. Chonoles Imlay, S. Korshunov, and J.A. Imlay. Physiological roles and adverse effects of the two cystine importers of *Escherichia coli*. *J. Bacteriol.*, 197:3629–3644, 2015.
- [112] G. Inesi, T. Watanabe, C. Coan, and A. Murphy. The mechanism of sarcoplasmic reticulum ATPase. *Ann. N.Y. Acad. Sci.*, 402:515–532, 1982.
- [113] S. Jayakanthan, S.A. Roberts, A. Weichsel, J.M. Arguello, and M.M. McEvoy. Conformations of the apo-, substrate-bound and phosphate-bound ATP-binding domain of the Cu(II) ATPase CopB illustrate coupling of domain movement to the catalytic cycle. *Biosci Rep*, 32:443–453, 2012.
- [114] W. Jekabsons and W. Schuster. *orf250* encodes a second subunit of an ABC-type heme transporter in *Oenothera* mitochondria. *Mol. Gen. Genet.*, 246:166–173, 1995.
- [115] M.S. Jensen, S.R. Costa, A.S. Duelli, P.A. Andersen, L.R. Poulsen, L.D. Stanchev, P. Gourdon, M. Palmgren, T. Günther Pomorski, and R.L. Lopez-Marques. Phospholipid flipping involves a central cavity in P4 ATPases. *Sci. Rep.*, 7:17621–17621, 2017.
- [116] T. Johansson, C. Oswald, A. Pedersen, S. Tornroth, M. Okvist, B.G. Karlsson, J. Rydstrom, and U. Krengel. X-ray structure of domain I of the proton-pumping membrane protein transhydrogenase from *Escherichia coli*. *J. Mol. Biol.*, 352:299–312, 2005.
- [117] K. Kamijo, S. Taketani, S. Yokota, T. Osumi, and T. Hashimoto. The 70-kDa peroxisomal membrane protein is a member of the Mdr (P-glcoprotein)-related ATP-binding protein superfamily. *J. Biol. Chem.*, 265:4534–4540, 1990.
- [118] M. Karow and C. Georgopoulos. The essential *Escherichia coli msbA* gene, a multicopy suppressor of null mutations in the *htrB* gene, is related to the universally conserved family of ATP-dependent translocators. *Mol. Microbiol.*, 7:69–79, 1993.
- [119] K. Kashiwagi, S. Miyamoto, E. Nukui, H. Kobayashi, and K. Igarashi. Functions of *potA* and *potD* proteins in spermidine - preferential uptake system in *Escherichia coli*. *J. Biol. Chem.*, 268:19358–19363, 1993.

- [120] J.A. Keightley, B.H. Zimmermann, M.W. Mather, P. Springer, A. Pastuszyn, D.M. Lawrence, and J.A. Fee. Molecular genetic and protein chemical characterization of the cytochrome *ba₃* from *Thermus thermophilus* HB8. *J. Biol. Chem.*, 270:20345–20358, 1995.
- [121] D. Keilin and E.F. Hartree. Cytochrome oxidase. *Proc. R. Soc. Lond. B Biol. Sci.*, 125:171–186, 1938.
- [122] D. Keilin and E.F. Hartree. Cytochrome and cytochrome oxidase. *Proc. R. Soc. Lond. B Biol. Sci.*, 127:167–191, 1939.
- [123] B. Kempf, J. Gade, and E. Bremer. Lipoprotein from the osmoregulated ABC transport system OpuA of *Bacillus subtilis*: purification of the glycine betaine binding protein and characterization of a functional lipidless mutant. *J. Bacteriol.*, 179:6213–6220, 1997.
- [124] D. Keppler, J. König, and M. Buchler. The canalicular multidrug resistance protein, cMRP/MRP2, a novel conjugate export pump expressed in the apical membrane of hepatocytes. *Adv. Enzyme Regul.*, 37:321–333, 1997.
- [125] M.A. Kertesz. Bacterial transporters for sulfate and organosulfur compounds. *Res. Microbiol.*, 152:279–290, 2001.
- [126] H.H. Khun, S.D. Kirby, and B.C. Lee. A *Neisseria meningitidis* fbp ABC mutant is incapable of using nonheme iron for growth. *Infect. Immun.*, 66:2330–2336, 1998.
- [127] C. Kim, S. Song, and C. Park. The D-allose operon of *Escherichia coli* K-12. *J. Bacteriol.*, 179:7631–7637, 1997.
- [128] Y.S. Kim. Malonate metabolism: biochemistry, molecular biology, physiology, and industrial application. *J. Biochem. Mol. Biol.*, 35:443–451, 2002.
- [129] C. Klein and K.D. Entian. Genes involved in self-protection against the lantibiotic subtilin produced by *Bacillus subtilis* ATCC 6633. *Appl. Environ. Microbiol.*, 60:2793–2801, 1994.
- [130] P.E. Kolenbrander, R.N. Andersen, R.A. Baker, and H.F. Jenkinson. The adhesion-associated *aca* operon in *Streptococcus gordonii* encodes an inducible high-affinity ABC transporter for Mn²⁺ uptake. *J. Bacteriol.*, 180:290–295, 1998.
- [131] L. Komorowski, W. Verheyen, and G. Schafer. The archaeal respiratory supercomplex SoxM from *S. acidocaldarius* combines features of quinole and cytochrome *c* oxidases. *Biol. Chem.*, 383:1791–1799, 2002.
- [132] W. Koster. Iron(III) hydroxamate transport across the cytoplasmic membrane of *Escherichia coli*. *Biol. Met.*, 4:23–32, 1991.
- [133] G. Kuan, E. Dassa, N. Saurin, M., Saier Hofnung, , and Jr. Phylogenetic analyses of the ATP-binding constituents of bacterial extracytoplasmic receptor-dependent ABC-type nutrient uptake permeases. *Res. Microbiol.*, 146:271–278, 1995.
- [134] C.R. Lancaster. *Wolinella succinogenes* quinol:fumarate reductase-2.2-A resolution crystal structure and the E-pathway hypothesis of coupled transmembrane proton and electron transfer. *Biochim. Biophys. Acta*, 1565:215–231, 2002.
- [135] C.R. Lancaster. The di-heme family of respiratory complex II enzymes. *Biochim. Biophys. Acta*, 1827:679–687, 2013.
- [136] C.R. Lancaster, E. Herzog, H.D. Juhnke, M.G. Madej, F.G. Muller, R. Paul, and P.G. Schleidt. Electroneutral and electrogenic catalysis by dihaem-containing succinate:quinone oxidoreductases. *Biochem Soc Trans.*, 36:996–1000, 2008.
- [137] T.G. Laughlin, A.N. Bayne, J.F. Trempe, D.F. Savage, and K.M. Davies. Structure of the complex I-like molecule NDH of oxygenic photosynthesis. *Nature*, 566:411–414, 2019.
- [138] M. Lauraeus and M. Wikstrom. The terminal quinol oxidases of *Bacillus subtilis* have different energy conservation properties. *J. Biol. Chem.*, 268:11470–11473, 1993.
- [139] D. Lautier, Y. Canitrot, R.G. Deeley, and S.P. Cole. Multidrug resistance mediated by the multidrug resistance protein (MRP) gene. *Biochem. Pharmacol.*, 52:967–977, 1996.
- [140] V. Lazarevic and D. Karamoto. The tagGH operon of *Bacillus subtilis* 168 encodes a two-component ABC transporter involved in the metabolism of two wall teichoic acids. *Mol. Microbiol.*, 16:345–355, 1995.
- [141] E. Lemma, J. Simon, H. Schagger, and A. Kroger. Properties of the menaquinol oxidase (Qox) and of qox deletion mutants of *Bacillus subtilis*. *Arch. Microbiol.*, 163:432–438, 1995.

- [142] T. Lenn, M.C. Leake, and C.W. Mullineaux. Clustering and dynamics of cytochrome *bd*-I complexes in the *Escherichia coli* plasma membrane *in vivo*. *Mol. Microbiol.*, 70:1397–1407, 2008.
- [143] S. Letoffe, P. Delepelaire, and C. Wandersman. Protease secretion by *Erwinia chrysanthemi*: the specific secretion functions are analogous to those of *Escherichia coli* α -haemolysin. *EMBO J.*, 9:1375–1382, 1990.
- [144] D. Lewis, R. Pilankatta, G. Inesi, G. Bartolommei, M.R. Moncelli, and F. Tadini-Buoninsegni. Distinctive features of catalytic and transport mechanisms in mammalian sarco-endoplasmic reticulum Ca^{2+} ATPase (SERCA) and Cu^{+} (ATP7A/B) ATPases. *J. Biol. Chem.*, 287:32717–32727, 2012.
- [145] X. Li, W. Zhuo, J. Yu, J. Ge, J. Gu, Y. Feng, M. Yang, L. Wang, and N. Wang. Structure of the nucleotide-binding domain of a dipeptide ABC transporter reveals a novel iron-sulfur cluster-binding domain. *Acta Crystallogr. D Biol. Crystallogr.*, 69:256–265, 2013.
- [146] Z.S. Li, M. Szczycka, Y.P. Lu, D.J. Thiele, and P.A. Rea. The yeast cadmium factor protein (YCF1) is a vacuolar glutathione *S*-conjugate pump. *J. Biol. Chem.*, 271:6509–6517, 1996.
- [147] K.J. Linton and C.F. Higgins. The *Escherichia coli* ATP-binding cassette (ABC) proteins. *Mol. Microbiol.*, 28:5–13, 1998.
- [148] D.W. Loe, R.G. Deeley, and S.P. Cole. Characterization of vincristine transport by the M_r 190,000 multidrug resistance protein (MRP): evidence for cotransport with reduced glutathione. *Cancer Res.*, 58:5130–5136, 1998.
- [149] R.L. Lopez-Marques, L.R. Poulsen, S. Hanisch, K. Meffert, M.J. Buch-Pedersen, M.K. Jakobsen, T.G. Pomorski, and M.G. Palmgren. Intracellular targeting signals and lipid specificity determinants of the ALA/ALIS P4-ATPase complex reside in the catalytic ALA α -subunit. *Mol. Biol. Cell*, 21:791–801, 2010.
- [150] Y.P. Lu, Z.S. Li, and P.A. Rea. AtMRP1 gene of *Arabidopsis* encodes a glutathione *S*-conjugate pump: isolation and functional definition of a plant ATP-binding cassette transporter gene. *Proc. Natl. Acad. Sci. USA*, 94:8243–8248, 1997.
- [151] H.H. Luoto, G.A. Belogurov, A.A. Baykov, R. Lahti, and A.M. Malinen. Na^{+} -translocating membrane pyrophosphatases are widespread in the microbial world and evolutionarily precede H^{+} -translocating pyrophosphatases. *J. Biol. Chem.*, 286:21633–21642, 2011.
- [152] W. Ma and T. Ogawa. Oxygenic photosynthesis-specific subunits of cyanobacterial NADPH dehydrogenases. *IUBMB Life*, 67:3–8, 2015.
- [153] S.M. Mackenzie, M.R. Brooker, T.R. Gill, G.B. Cox, A.J. Howells, and G.D. Ewart. Mutations in the white gene of *Drosophila melanogaster* affecting ABC transporters that determine eye colouration. *Biochim. Biophys. Acta*, 1419:173–185, 1999.
- [154] D.H. MacLennan, W.J. Rice, and N.M. Green. The mechanism of Ca^{2+} transport by sarco(endo)plasmic reticulum Ca^{2+} -ATPases. *J. Biol. Chem.*, 272:28815–28818, 1997.
- [155] M.G. Madej, H.R. Nasiri, N.S. Hilgendorff, H. Schwalbe, G. Uden, and C.R. Lancaster. Experimental evidence for proton motive force-dependent catalysis by the diheme-containing succinate:menaquinone oxidoreductase from the Gram-positive bacterium *Bacillus licheniformis*. *Biochemistry*, 45:15049–15055, 2006.
- [156] M.E. Maguire. MgtA and MgtB: prokaryotic P-type ATPases that mediate Mg^{2+} influx. *J. Bioenerg. Biomembr.*, 24:319–328, 1992.
- [157] Y. Mahé, Y. Lemoine, and K. Kuchler. The ATP-binding cassette transporters Pdr5 and Snq2 of *Saccharomyces cerevisiae* can mediate transport of steroids *in vivo*. *J. Biol. Chem.*, 271:25167–25172, 1996.
- [158] K. Makdessi, J.R. Andreesen, and A. Pich. Tungstate uptake by a highly specific ABC transporter in *Eubacterium acidaminophilum*. *J. Biol. Chem.*, 276:24557–24564, 2001.
- [159] A.M. Malinen, G.A. Belogurov, A.A. Baykov, and R. Lahti. Na^{+} -pyrophosphatase: a novel primary sodium pump. *Biochemistry*, 46:8872–8878, 2007.
- [160] S. Mana-Capelli, A.K. Mandal, and J.M. Arguello. *Archaeoglobus fulgidus* CopB is a thermophilic Cu^{2+} -ATPase: functional role of its histidine-rich-*N*-terminal metal binding domain. *J. Biol. Chem.*, 278:40534–40541, 2003.

- [161] A.K. Mandal and J.M. Arguello. Functional roles of metal binding domains of the *Archaeoglobus fulgidus* Cu⁺-ATPase CopA. *Biochemistry*, 42:11040–11047, 2003.
- [162] C.A.M. Marres and E.C. Slater. Polypeptide composition of purified QH₂:cytochrome *c* oxidoreductase from beef-heart mitochondria. *Biochim. Biophys. Acta*, 462:531–548, 1977.
- [163] A. Martinez, P. Ostrovsky, and D.N. Nunn. Identification of an additional member of the secretin superfamily of proteins in *Pseudomonas aeruginosa* that is able to function in type II protein secretion. *Mol. Microbiol.*, 28:1235–1246, 1998.
- [164] D. Mattle, O. Sitsel, H.E. Autzen, G. Meloni, P. Gourdon, and P. Nissen. On allosteric modulation of P-type Cu⁺-ATPases. *J. Mol. Biol.*, 425:2299–2308, 2013.
- [165] A.T. McKie, D. Barrow, G.O. Latunde-Dada, A. Rolfs, G. Sager, E. Mudaly, M. Mudaly, C. Richardson, D. Barlow, A. Bomford, T.J. Peters, K.B. Raja, S. Shirali, M.A. Hediger, F. Farzaneh, and R.J. Simpson. An iron-regulated ferric reductase associated with the absorption of dietary iron. *Science*, 291:1755–1759, 2001.
- [166] J. Meccas and E.J. Strauss. Molecular mechanisms of bacterial virulence: type III secretion and pathogenicity islands. *Emerg. Infect. Diseases.*, 2:270–288, 1996.
- [167] E. Meimaridou, J. Kowalczyk, L. Guasti, C.R. Hughes, F. Wagner, P. Frommolt, P. Nurnberg, N.P. Mann, R. Banerjee, H.N. Saka, J.P. Chapple, P.J. King, A.J. Clark, and L.A. Metherell. Mutations in NNT encoding nicotinamide nucleotide transhydrogenase cause familial glucocorticoid deficiency. *Nat. Genet.*, 44:740–742, 2012.
- [168] C. Merlin, G. Gardiner, S. Durand, and M. Masters. The *Escherichia coli* *metD* locus encodes an ABC transporter which includes Abc (MetN), YaeE (MetI), and YaeC (MetQ). *J. Bacteriol.*, 184:5513–5517, 2002.
- [169] S. Michaelis. STE6, the yeast α -factor exporter. *Semin. Cell Biol.*, 4:17–27, 1993.
- [170] J. Micklefield, K.J. Harris, S. Gröger, U. Mocek, H. Hilbi, P. Dimroth, and H.G. Floss. Stereochemical course of malonate decarboxylase in *Malonomonas rubra* has biotin decarboxylation with retention. *J. Am. Chem. Soc.*, 117:1153–1154, 1995.
- [171] M.J. Miller, M. Hermodson, and R.B. Gennis. The active form of the cytochrome *d* terminal oxidase complex of *Escherichia coli* is a heterodimer containing one copy of each of the two subunits. *J. Biol. Chem.*, 263:5235–5240, 1988.
- [172] R.F. Mills, A. Francini, P.S. Ferreira da Rocha, P.J. Baccarini, M. Aylett, G.C. Krijger, and L.E. Williams. The plant P1B-type ATPase AtHMA4 transports Zn and Cd and plays a role in detoxification of transition metals supplied at elevated levels. *FEBS Lett.*, 579:783–791, 2005.
- [173] F. Momburg, J. Roelse, J.C. Howard, G.W. Butcher, G.J. Hammerling, and J.J. Neefjes. Selectivity of MHC-encoded peptide transporters from human, mouse and rat. *Nature*, 367:648–651, 1994.
- [174] M.B. Morris, M.E. Auland, Y.H. Xu, and B.D. Roufogalis. Characterization of the Mg²⁺-ATPase activity of the human erythrocyte membrane. *Biochem. Mol. Biol. Int.*, 31:823–832, 1993.
- [175] A. Moussatova, C. Kandt, M.L. O'Mara, and D.P. Tieleman. ATP-binding cassette transporters in *Escherichia coli*. *Biochim. Biophys. Acta*, 1778:1757–1771, 2008.
- [176] F.H. Muller, T.M. Bandejas, T. Urich, M. Teixeira, C.M. Gomes, and A. Kletzin. Coupling of the pathway of sulphur oxidation to dioxygen reduction: characterization of a novel membrane-bound thiosulphate:quinone oxidoreductase. *Mol. Microbiol.*, 53:1147–1160, 2004.
- [177] K. Nagao, Y. Taguchi, M. Arioka, H. Kadokura, A. Takatsuki, K. Yoda, and M. Yamasaki. *bfr1*⁺, a novel gene of *Schizosaccharomyces pombe* which confers brefeldin A resistance, is structurally related to the ATP-binding cassette superfamily. *J. Bacteriol.*, 177:1536–1543, 1995.
- [178] M. Nakai, A. Goto, T. Nohara, D. Sugito, and T. Endo. Identification of the SecA protein homolog in pea chloroplasts and its possible involvement in thylakoidal protein transport. *J. Biol. Chem.*, 269:31338–33341, 1994.
- [179] Y. Nakayama, M. Hayashi, and T. Unemoto. Identification of six subunits constituting Na⁺-translocating NADH-quinone reductase from the marine *Vibrio alginolyticus*. *FEBS Lett.*, 422:240–242, 1998.

- [180] S. Narita and H. Tokuda. Biochemical characterization of an ABC transporter LptBFGC complex required for the outer membrane sorting of lipopolysaccharides. *FEBS Lett.*, 583:2160–2164, 2009.
- [181] M. Nijenhuis and G.J. Hammerling. Multiple regions of the transporter associated with antigen processing (TAP) contribute to its peptide binding site. *J. Immunol.*, 157:5467–5477, 1996.
- [182] K. Nikaido, P.Q. Liu, and G. Ferro-Luzzi Ames. Purification and characterization of HisP, the ATP-binding subunit of a traffic ATPase (ABC transporter), the histidine permease of *Salmonella typhimurium*. Solubilization, dimerization, and ATPase activity. *J. Biol. Chem.*, 272:27745–27752, 1997.
- [183] H. Noji, R. Yasuda, M. Kinoshita Yoshida, and Jr. Direct observation of the rotation of F₁-ATPase. *Nature*, 386:299–302, 1997.
- [184] R. Novak, J.S. Braun, E. Charpentier, and E. Tuomanen. Penicillin tolerance genes of *Streptococcus pneumoniae*: the ABC-type manganese permease complex Psa. *Mol. Microbiol.*, 29:1285–1296, 1998.
- [185] M. Ogura, K. Tsukahara, K. Hayashi, and T. Tanaka. The *Bacillus subtilis* NatK-NatR two-component system regulates expression of the *natAB* operon encoding an ABC transporter for sodium ion extrusion. *Microbiology*, 153:667–675, 2007.
- [186] S. Okuda, E. Freinkman, and D. Kahne. Cytoplasmic ATP hydrolysis powers transport of lipopolysaccharide across the periplasm in *E. coli*. *Science*, 338:1214–1217, 2012.
- [187] T. Omata. Structure, function and regulation of the nitrate transport system of the cyanobacterium *Synechococcus* sp. PCC7942. *Plant Cell Physiol.*, 36:207–213, 1995.
- [188] T. Padilla-Benavides, J.E. Long, D. Raimunda, C.M. Sasseti, and J.M. Arguello. A novel P(1B)-type Mn²⁺-transporting ATPase is required for secreted protein metallation in mycobacteria. *J. Biol. Chem.*, 288:11334–11347, 2013.
- [189] S.I. Patzer and K. Hantke. The ZnuABC high-affinity zinc uptake system and its regulator Zur in *Escherichia coli*. *Mol. Microbiol.*, 28:1199–1210, 1998.
- [190] I.T. Paulsen, A.M. Saier Beness, and Jr. Computer-based analysis of the protein constituents of transport systems catalysing export of complex carbohydrates in bacteria. *Microbiology*, 143:2685–2699, 1997.
- [191] S.R. Pearce, M.L. Mimmack, M.P. Gallagher, U. Gileadi, S.C. Hyde, and C.F. Higgins. Membrane topology of the integral membrane components, OppB and OppC, of the oligopeptide permease of *Salmonella typhimurium*. *Mol. Microbiol.*, 6:47–57, 1992.
- [192] G. Peltier, E.M. Aro, and T. Shikanai. NDH-1 and NDH-2 plastoquinone reductases in oxygenic photosynthesis. *Annu. Rev. Plant Biol.*, 67:55–80, 2016.
- [193] D.S. Perlin, M.J. San Francisco, C.W. Slayman, and B.P. Rosen. H⁺/ATP stoichiometry of proton pumps from *Neurospora crassa* and *Escherichia coli*. *Arch. Biochem. Biophys.*, 248:53–61, 1986.
- [194] R.P. Pigeon and R.P. Silver. Analysis of the G93E mutant allele of KpsM, the membrane component of an ABC transporter involved in polysialic acid translocation in *Escherichia coli* K1. *FEMS Microbiol. Lett.*, 156:217–222, 1997.
- [195] R. Pistocchi, K. Kashiwagi, S. Miyamoto, E. Nukui, Y. Sadakata, H. Kobayashi, and K. Igarashi. Characteristics of the operon for a putrescine transport system that maps at 19 minutes on the *Escherichia coli* chromosome. *J. Biol. Chem.*, 268:146–152, 1993.
- [196] D. Pletzer, C. Lafon, Y. Braun, T. Kohler, M.G. Page, M. Mourez, and H. Weingart. High-throughput screening of dipeptide utilization mediated by the ABC transporter DppBCDF and its substrate-binding proteins DppA¹-A⁵ in *Pseudomonas aeruginosa*. *PLoS One*, 9:e111311–e111311, 2014.
- [197] R.L. Post, A.K. Sen, and A.S. Rosenthal. A phosphorylated intermediate in adenosine triphosphate-dependent sodium and potassium transport across kidney membrane. *J. Biol. Chem.*, 240:1437–1445, 1965.
- [198] R. Prasad, P. De Wergifosse, A. Goffeau, and E. Balzi. Molecular cloning and characterization of a novel gene of *Candida albicans*, CDR1, conferring multiple resistance to drugs and antifungals. *Curr. Genet.*, 27:320–329, 1995.
- [199] W.G. Purschke, C.L. Schmidt, A. Petersen, and G. Schafer. The terminal quinol oxidase of the hyperthermophilic archaeon *Acidianus ambivalens* exhibits a novel subunit structure and gene organization. *J. Bacteriol.*, 179:1344–1353, 1997.

- [200] A. Puustinen, M. Finel, T. Haltia, R.B. Gennis, and M. Wikstrom. Properties of the two terminal oxidases of *Escherichia coli*. *Biochemistry*, 30:3936–3942, 1991.
- [201] R., Saier Tam, , and Jr. Structural, functional, and evolutionary relationships among extracellular solute-binding receptors of bacteria. *Microbiol. Rev.*, 57:320–346, 1993.
- [202] E.C. Rabon and M.A. Reuben. The mechanism and structure of the gastric H,K-ATPase. *Annu. Rev. Physiol.*, 52:321–344, 1990.
- [203] S. Rahlfs and V. Müller. Sequence of subunit *c* of the Na⁺-translocating F₁F_o-ATPase of *Acetobacterium woodii*: proposal for determinants of Na⁺ specificity as revealed by sequence comparisons. *FEBS Lett.*, 404:269–271, 1997.
- [204] T.M. Ramseier, H.V. Winteler, and H. Hennecke. Discovery and sequence analysis of bacterial genes involved in the biogenesis of *c*-type cytochromes. *J. Biol. Chem.*, 266:7793–7803, 1991.
- [205] P.A. Rea and R.J. Poole. Chromatographic resolution of H⁺-translocating pyrophosphatase from H⁺-translocating ATPase of higher plant tonoplast. *Plant Physiol.*, 81:126–129, 1986.
- [206] C. Rensing, B. Mitra, and B.P. Rosen. The *zntA* gene of *Escherichia coli* encodes a Zn(II)-translocating P-type ATPase. *Proc. Natl. Acad. Sci. USA*, 94:14326–14331, 1997.
- [207] C. Rensing, Y. Sun, B. Mitra, and B.P. Rosen. Pb(II)-translocating P-type ATPases. *J. Biol. Chem.*, 273:32614–32617, 1998.
- [208] J.S. Rieske. Composition, structure, and function of complex III of the respiratory chain. *Biochim. Biophys. Acta*, 456:195–247, 1976.
- [209] B.P. Rosen, U. Weigel, R.A. Monticello, and B.P. Edwards. Molecular analysis of an anion pump: purification of the ArsC protein. *Arch. Biochem. Biophys.*, 284:381–385, 1991.
- [210] N. Ruiz, L.S. Gronenberg, D. Kahne, and T.J. Silhavy. Identification of two inner-membrane proteins required for the transport of lipopolysaccharide to the outer membrane of *Escherichia coli*. *Proc. Natl. Acad. Sci. USA*, 105:5537–5542, 2008.
- [211] G. Sachs, R.H. Collier, R.L. Shoemaker, and B.I. Hirschowitz. The energy source for gastric H⁺ secretion. *Biochim. Biophys. Acta*, 162:210–219, 1968.
- [212] Saier and Jr. , Tam. R., Reizer, A. and Reizer, J. Two novel families of bacterial membrane proteins concerned with nodulation, cell division and transport. *Mol. Microbiol.*, 11:841–847, 1994.
- [213] Saier and Jr. Molecular phylogeny as a basis for the classification of transport proteins from bacteria, archaea and eukarya. *Adv. Microb. Physiol.*, 40:81–136, 1998.
- [214] Y. Sanz, F.C. Lanfermeijer, P. Renault, A. Bolotin, W.N. Konings, and B. Poolman. Genetic and functional characterization of *dpp* genes encoding a dipeptide transport system in *Lactococcus lactis*. *Arch. Microbiol.*, 175:334–343, 2001.
- [215] V. Sarafian and R.J. Poole. Purification of an H⁺-translocating inorganic pyrophosphatase from vacuole membranes of red beet. *Plant Physiol.*, 91:34–38, 1989.
- [216] U. Sauer, F. Canonaco, S. Heri, A. Perrenoud, and E. Fischer. The soluble and membrane-bound transhydrogenases UdhA and PntAB have divergent functions in NADPH metabolism of *Escherichia coli*. *J. Biol. Chem.*, 279:6613–6619, 2004.
- [217] H.J. Schatzmann and F.F. Vicenzi. Calcium movements across the membrane of human red cells. *J. Physiol.*, 201:369–395, 1969.
- [218] R. Schuch and A.T. Maurelli. The *mxi*-*Spa* type III secretory pathway of *Shigella flexneri* requires an outer membrane lipoprotein, MxiM, for invasins translocation. *Infect. Immun.*, 67:1982–1991, 1999.
- [219] J.M. Schuller, J.A. Birrell, H. Tanaka, T. Konuma, H. Wulfhorst, N. Cox, S.K. Schuller, J. Thiemann, W. Lubitz, P. Setif, T. Ikegami, B.D. Engel, G. Kurisu, and M.M. Nowaczyk. Structural adaptations of photosynthetic complex I enable ferredoxin-dependent electron transfer. *Science*, 363:257–260, 2019.
- [220] S.V. Scott and S.M. Theg. A new chloroplast protein import intermediate reveals distinct translocation machineries in the two envelope membranes: energetics and mechanistic implications. *J. Cell Biol.*, 132:63–75, 1996.

- [221] J.B. Scripture, C. Voelker, S. Miller, R.T. O'Donnell, L. Polgar, J. Rade, B.F. Horazdovsky, and R.W. Hogg. High-affinity L-arabinose transport operon. Nucleotide sequence and analysis of gene products. *J. Mol. Biol.*, 197:37–46, 1987.
- [222] S. Segami, T. Tomoyama, S. Sakamoto, S. Gunji, M. Fukuda, S. Kinoshita, N. Mitsuda, A. Ferjani, and M. Maeshima. Vacuolar H⁺-pyrophosphatase and cytosolic soluble pyrophosphatases cooperatively regulate pyrophosphate levels in *Arabidopsis thaliana*. *Plant Cell*, 30:1040–1061, 2018.
- [223] R. Serrano, M.C. Kielland-Brandt, and G.R. Fink. Yeast plasma membrane ATPase is essential for growth and has homology with (Na⁺+K⁺)-, K⁺-and Ca²⁺-ATPases. *Nature*, 319:689–693, 1986.
- [224] R. Serrano and F. Portillo. Catalytic and regulatory sites of yeast plasma membrane H⁺-ATPase studied by directed mutagenesis. *Biochim. Biophys. Acta*, 1018:195–199, 1990.
- [225] C.M. Shea and M.A. McIntosh. Nucleotide sequence and genetic organization of the ferric enterobactin transport system: homology to other periplasmic binding-protein-dependent systems in *Escherichia coli*. *Mol. Microbiol.*, 5:1415–1428, 1991.
- [226] M. Shepherd, G. Sanguinetti, G.M. Cook, and R.K. Poole. Compensations for diminished terminal oxidase activity in *Escherichia coli*: cytochrome *bd-II*-mediated respiration and glutamate metabolism. *J. Biol. Chem.*, 285:18464–18472, 2010.
- [227] A. Siebers and K. Altendorf. Characterization of the phosphorylated intermediate of the K⁺-translocating Kdp-ATPase from *Escherichia coli*. *J. Biol. Chem.*, 264:5831–5838, 1989.
- [228] S. Silver and G. Ji. Newer systems for bacterial resistance to toxic heavy metals. *Environ. Health Perspect.* 102, Suppl., 3:107–113, 1994.
- [229] S. Silver, T.K. Misra, and R.A. Laddaga. DNA sequence analysis of bacterial toxic heavy metal resistance. *Biol. Trace Elem. Res.*, 21:145–163, 1989.
- [230] H. Singh, S. Velamakanni, M.J. Deery, J. Howard, S.L. Wei, and H.W. van Veen. ATP-dependent substrate transport by the ABC transporter MsbA is proton-coupled. *Nat. Commun.*, 7:12387–12387, 2016.
- [231] A. Sirko, M. Zatyka, E. Sadowy, and D. Hulanicka. Sulfate and thiosulfate transport in *Escherichia coli* K-12: evidence for a functional overlapping of sulfate- and thiosulfate-binding proteins. *J. Bacteriol.*, 177:4134–4136, 1995.
- [232] J.C. Skou. The influence of some cations on an adenosinetriphosphatase from peripheral nerve. *Biochim. Biophys. Acta*, 23:394–401, 1957.
- [233] J.C. Skou. The energy-coupled exchange of Na⁺ for K⁺ across the cell membrane. The Na⁺,K⁺ pump. *FEBS Lett.*, 268:314–324, 1990.
- [234] J.P. Smart, M.J. Cliff, and D.J. Kelly. A role for tungsten in the biology of *Campylobacter jejuni*: tungstate stimulates formate dehydrogenase activity and is transported via an ultra-high affinity ABC system distinct from the molybdate transporter. *Mol. Microbiol.*, 74:742–757, 2009.
- [235] M.D. Snavelly, C.G. Miller, and M.E. Maguire. The *mgtB* Mg²⁺ transport locus of *Salmonella typhimurium* encodes a P-type ATPase. *J. Biol. Chem.*, 266:815–823, 1991.
- [236] M. Solioz and K. Davies. Operon of vacuolar-type Na⁺-ATPase of *Enterococcus hirae*. *J. Biol. Chem.*, 269:9453–9459, 1994.
- [237] N. Sone, N. Tsuchiya, M. Inoue, and S. Noguchi. *Bacillus stearothermophilus* *qcr* operon encoding rieske FeS protein, cytochrome *b₆*, and a novel-type cytochrome *c₁* of quinol-cytochrome *c* reductase. *J. Biol. Chem.*, 271:12457–12462, 1996.
- [238] S. Song and C. Park. Organization and regulation of the D-xylose operons in *Escherichia coli* K-12: XylR acts as a transcriptional activator. *J. Bacteriol.*, 179:7025–7032, 1997.
- [239] P. Sperandio, R. Cescutti, R. Villa, C. Di Benedetto, D. Candia, G. Deho, and A. Polissi. Characterization of *lptA* and *lptB*, two essential genes implicated in lipopolysaccharide transport to the outer membrane of *Escherichia coli*. *J. Bacteriol.*, 189:244–253, 2007.

- [240] C.D. Speziali, S.E. Dale, J.A. Henderson, E.D. Vines, and D.E. Heinrichs. Requirement of *Staphylococcus aureus* ATP-binding cassette-ATPase FhuC for iron-restricted growth and evidence that it functions with more than one iron transporter. *J. Bacteriol.*, 188:2048–2055, 2006.
- [241] H. Staudenmaier, B. Van Hove, Z. Yaraghi, and V. Braun. Nucleotide sequences of the fecBCDE genes and locations of the proteins suggest a periplasmic-binding-protein-dependent transport mechanism for iron(III) dicitrate in *Escherichia coli*. *J. Bacteriol.*, 171:2626–2633, 1989.
- [242] M. Steglich, J.D. Hofmann, J. Helmecke, J. Sikorski, C. Sproer, T. Riedel, B. Bunk, J. Overmann, M. Neumann-Schaal, and U. Nubel. Convergent loss of ABC transporter genes from *Clostridioides difficile* genomes is associated with impaired tyrosine uptake and *p*-cresol production. *Front. Microbiol.*, 9:901–901, 2018.
- [243] F. Stenberg, G. von Heijne, and D.O. Daley. Assembly of the cytochrome *bo*₃ complex. *J. Mol. Biol.*, 371:765–773, 2007.
- [244] D. Su and H. Asard. Three mammalian cytochromes *b*₅₆₁ are ascorbate-dependent ferrireductases. *FEBS J.*, 273:3722–3734, 2006.
- [245] D.T. Sullivan, L.A. Bell, D.R. Paton, and M.C. Sullivan. Purine transport by malpighian tubules of pteridine-deficient eye color mutants of *Drosophila melanogaster*. *Biochem. Genet.*, 17:565–573, 1979.
- [246] H. Suzuki, M. Kamakura, M. Morii, and N. Takeguchi. The phospholipid flippase activity of gastric vesicles. *J. Biol. Chem.*, 272:10429–10434, 1997.
- [247] H. Suzuki, T. Koyanagi, S. Izuka, A. Onishi, and H. Kumagai. The *yliA*, -B, -C, and -D genes of *Escherichia coli* K-12 encode a novel glutathione importer with an ATP-binding cassette. *J. Bacteriol.*, 187:5861–5867, 2005.
- [248] F. Tadini-Buoninsegni, G. Bartolommei, M.R. Moncelli, R. Pilankatta, D. Lewis, and G. Inesi. ATP dependent charge movement in ATP7B Cu⁺-ATPase is demonstrated by pre-steady state electrical measurements. *FEBS Lett.*, 584:4619–4622, 2010.
- [249] M.E. Taga, J.L. Semmelhack, and B.L. Bassler. The LuxS-dependent autoinducer AI-2 controls the expression of an ABC transporter that functions in AI-2 uptake in *Salmonella typhimurium*. *Mol. Microbiol.*, 42:777–793, 2001.
- [250] K. Takase, S. Kakinuma, I. Yamato, K. Konishi, K. Igarashi, and Y. Kanikuma. Sequencing and characterization of the *ntp* gene cluster for vacuolar-type Na⁺-translocating ATPase of *Enterococcus hirae*. *J. Biol. Chem.*, 269:11037–11044, 1994.
- [251] T. Tao, M.D. Snavely, S.G. Farr, and M.E. Maguire. Magnesium transport in *Salmonella typhimurium*: *mtgA* encodes a P-type ATPase and is regulated by Mg²⁺ in a manner similar to that of the *mgtB* P-type ATPase. *J. Bacteriol.*, 177:2654–2662, 1995.
- [252] R.G. Tearle, J.M. Belote, M. McKeown, B.S. Baker, and A.J. Howells. Cloning and characterization of the scarlet gene of *Drosophila melanogaster*. *Genetics*, 122:595–606, 1989.
- [253] Y. Terui, S.D. Saroj, A. Sakamoto, T. Yoshida, K. Higashi, S. Kurihara, H. Suzuki, T. Toida, K. Kashiwagi, and K. Igarashi. Properties of putrescine uptake by PotFGHI and PuuP and their physiological significance in *Escherichia coli*. *Amino Acids*, 46:661–670, 2014.
- [254] J.D. Thomas, P.J. Reeves, and G.P. Salmond. The general secretion pathway of *Erwinia carotovora* subsp. *carotovora*: analysis of the membrane topology of OutC and OutF. *Microbiology*, 143:713–720, 1997.
- [255] C. Toyoshima, M. Nakasako, H. Nomura, and H. Ogawa. Crystal structure of the calcium pump of sarcoplasmic reticulum at 2.6 Å resolution. *Nature*, 405:647–655, 2000.
- [256] A.X. Tran, C. Dong, and C. Whitfield. Structure and functional analysis of LptC, a conserved membrane protein involved in the lipopolysaccharide export pathway in *Escherichia coli*. *J. Biol. Chem.*, 285:33529–33539, 2010.
- [257] P.L. Tremblay, T. Zhang, S.A. Dar, C. Leang, and D.R. Lovley. The Rnf complex of *Clostridium ljungdahlii* is a proton-translocating ferredoxin:NAD⁺ oxidoreductase essential for autotrophic growth. *mBio*, 4:e00406–e00412, 2012.
- [258] K.J. Tsai and A.L. Linet. Formation of a phosphorylated enzyme intermediate by the *cadA* Cd²⁺-ATPase. *Arch. Biochem. Biophys.*, 305:267–270, 1993.

- [259] P. Turina, D. Samoray, and P. Graber. H⁺/ATP ratio of proton transport-coupled ATP synthesis and hydrolysis catalysed by CF₀F₁-liposomes. *EMBO J.*, 22:418–426, 2003.
- [260] J.R. van Der Ploeg, R. Iwanicka-Nowicka, T. Bykowski, M.M. Hryniewicz, and T. Leisinger. The *Escherichia coli* ssuEADCB gene cluster is required for the utilization of sulfur from aliphatic sulfonates and is regulated by the transcriptional activator Cbl. *J. Biol. Chem.*, 274:29358–29365, 1999.
- [261] J.R. van der Ploeg, M.A. Weiss, E. Saller, H. Nashimoto, N. Saito, M.A. Kertesz, and T. Leisinger. Identification of sulfate starvation-regulated genes in *Escherichia coli*: a gene cluster involved in the utilization of taurine as a sulfur source. *J. Bacteriol.*, 178:5438–5446, 1996.
- [262] H.W. van Veen and W.N. Konings. The ABC family of multidrug transporters in microorganisms. *Biochim. Biophys. Acta*, 1365:31–36, 1998.
- [263] W.P. Vermeulen, J.J. Briede, and B. Rolofsen. Manipulation of the phosphatidylethanolamine pool in the human red cell membrane affects its Mg²⁺-ATPase activity. *Mol. Membr. Biol.*, 13:95–102, 1996.
- [264] W. Voos, H. Martin, T. Krimmer, and N. Pfanner. Mechanisms of protein translocation into mitochondria. *Biochim. Biophys. Acta*, 1422:235–254, 1999.
- [265] M. Wagner, L. Shen, A. Albersmeier, N. van der Kolk, S. Kim, J. Cha, C. Braesen, J. Kalinowski, B. Siebers, and S.-V. Albers. *Sulfolobus acidocaldarius* transports pentoses via a carbohydrate uptake transporter 2 (CUT2)-type ABC transporter and metabolizes them through the aldolase-independent Weimberg pathway. *Appl. Environ. Microbiol.*, 84:e01273–17, 2018.
- [266] W.W. Wainio, B. Eichel, and A. Gould. Ion and pH optimum for the oxidation of ferrocycytochrome *c* by cytochrome *c* oxidase in air. *J. Biol. Chem.*, 235:1521–1525, 1960.
- [267] D.L. Walshaw, S. Lowthorpe, A. East, and P.S. Poole. Distribution of a sub-class of bacterial ABC polar amino acid transporter and identification of an N-terminal region involved in solute specificity. *FEBS Lett.*, 414:397–401, 1997.
- [268] L. Wang, P. Bradstock, C. Li, M.J. McInerney, and L.R. Krumholz. The role of Rnf in ion gradient formation in *Desulfovibrio alaskensis*. *PeerJ*, 4:e1919–e1919, 2016.
- [269] B.L. Wanner and W.W. Metcalf. Molecular genetic studies of a 10.9-kb operon in *Escherichia coli* for phosphonate uptake and biodegradation. *FEMS Microbiol. Lett.*, 79:133–139, 1992.
- [270] D.C. Webb, H. Rosenberg, and G.B. Cox. Mutational analysis of the *Escherichia coli* phosphate-specific transport system, a member of the traffic ATPase (or ABC) family of membrane transporters. A role for proline residues in transmembrane helices. *J. Biol. Chem.*, 267:24661–24668, 1992.
- [271] E. Webb, K. Claas, and D. Downs. *thiBPQ* encodes an ABC transporter required for transport of thiamine and thiamine pyrophosphate in *Salmonella typhimurium*. *J. Biol. Chem.*, 273:8946–8950, 1998.
- [272] S.A. White, S.J. Peake, S. McSweeney, G. Leonard, N.P. Cotton, and J.B. Jackson. The high-resolution structure of the NADP(H)-binding component (dIII) of proton-translocating transhydrogenase from human heart mitochondria. *Structure*, 8:1–12, 2000.
- [273] J. Wieland, A.M. Nitsche, J. Strayle, H. Steiner, and H.K. Rudolph. The PMR2 gene cluster encodes functionally distinct isoforms of a putative Na⁺ pump in the yeast plasma membrane. *EMBO J.*, 14:3870–3882, 1995.
- [274] M. Wikstrom and G. Hummer. Stoichiometry of proton translocation by respiratory complex I and its mechanistic implications. *Proc. Natl. Acad. Sci. USA*, 109:4431–4436, 2012.
- [275] M. Wikström, K. Krab, and M. Saraste. Proton-translocating cytochrome complexes. *Annu. Rev. Biochem.*, 50:623–655, 1981.
- [276] S.G. Williams, J.A. Greenwood, and C.W. Jones. Molecular analysis of the lac operon encoding the binding-protein-dependent lactose transport system and β-galactosidase in *Agrobacterium radiobacter*. *Mol. Microbiol.*, 6:1755–1768, 1992.
- [277] S. Wyman, R.J. Simpson, A.T. McKie, and P.A. Sharp. Dcytb (Cybrd1) functions as both a ferric and a cupric reductase *in vitro*. *FEBS Lett.*, 582:1901–1906, 2008.

- [278] K.B. Xavier and B.L. Bassler. Regulation of uptake and processing of the quorum-sensing autoinducer AI-2 in *Escherichia coli*. *J. Bacteriol.*, 187:238–248, 2005.
- [279] H. Yamamoto and T. Shikanai. In planta mutagenesis of Src homology 3 domain-like fold of NdhS, a ferredoxin-binding subunit of the chloroplast NADH dehydrogenase-like complex in *Arabidopsis*: a conserved Arg-193 plays a critical role in ferredoxin binding. *J. Biol. Chem.*, 288:36328–36337, 2013.
- [280] L.L. Yap, M.T. Lin, H. Ouyang, R.I. Samoilova, S.A. Dikanov, and R.B. Gennis. The quinone-binding sites of the cytochrome *bo₃* ubiquinol oxidase from *Escherichia coli*. *Biochim. Biophys. Acta*, 1797:1924–1932, 2010.
- [281] S.M. Yi, K.V. Narasimhulu, R.I. Samoilova, R.B. Gennis, and S.A. Dikanov. Characterization of the semiquinone radical stabilized by the cytochrome *aa₃-600* menaquinol oxidase of *Bacillus subtilis*. *J. Biol. Chem.*, 285:18241–18251, 2010.
- [282] T. Yonetani. Studies on cytochrome oxidase. II. Steady state properties. *J. Biol. Chem.*, 235:3138–3243, 1960.
- [283] T. Yonetani. Studies on cytochrome oxidase. III. Improved purification and some properties. *J. Biol. Chem.*, 236:1680–1688, 1961.
- [284] J. Yu and N.E. Le Brun. Studies of the cytochrome subunits of menaquinone:cytochrome *c* reductase (*bc* complex) of *Bacillus subtilis*. Evidence for the covalent attachment of heme to the cytochrome *b* subunit. *J. Biol. Chem.*, 273:8860–8866, 1998.
- [285] G.J. Zaman, M.J. Flens, M.R. van Leusden, M. de Haas, H.S. Mulder, J. Lankelma, H.M. Pinedo, R.J. Scheper, F. Baas, , H.J., and et al. The human multidrug resistance-associated protein MRP is a plasma membrane drug-efflux pump. *Proc. Natl. Acad. Sci. USA*, 91:8822–8826, 1994.
- [286] C. Zhang, J. Shuai, Z. Ran, J. Zhao, Z. Wu, R. Liao, J. Wu, W. Ma, and M. Lei. Structural insights into NDH-1 mediated cyclic electron transfer. *Nat. Commun.*, 11:888–888, 2020.
- [287] Z. Zhang, J.N. Feige, A.B. Chang, I.J. Anderson, V.M. Brodianski, A.G. Vitreschak, M.S., Saier Gelfand, , and Jr. A transporter of *Escherichia coli* specific for L- and D-methionine is the prototype for a new family within the ABC superfamily. *Arch. Microbiol.*, 180:88–100, 2003.
- [288] T. Zhou, B.P. Rosen, and D.L. Gatti. Crystallization and preliminary X-ray analysis of the catalytic subunit of the ATP-dependent arsenite pump encoded by the *Escherichia coli* plasmid R773. *Acta Crystallogr. D Biol. Crystallogr.*, 55:921–924, 1999.
- [289] Z. Zhou, K.A. White, A. Polissi, C. Georgopoulos, and C.R. Raetz. Function of *Escherichia coli* MsbA, an essential ABC family transporter, in lipid A and phospholipid biosynthesis. *J. Biol. Chem.*, 273:12466–12475, 1998.

Index

- ABC-type α -factor-pheromone transporter, 19
ABC-type β -glucan transporter, 22
ABC-type D-allose transporter, 23
ABC-type D-galactofuranose transporter, 24
ABC-type D-galactose transporter, 24
ABC-type D-ribose transporter, 23
ABC-type D-xylose transporter, 24
ABC-type D-xylose/L-arabinose transporter, 25
ABC-type L-arabinose transporter, 25
ABC-type aliphatic sulfonate transporter, 29
ABC-type antigen peptide transporter, 21
ABC-type autoinducer-2 transporter, 29
ABC-type capsular-polysaccharide transporter, 28
ABC-type Cd²⁺ transporter, 8
ABC-type cystine transporter, 21
ABC-type dipeptide transporter, 20
ABC-type fatty-acyl-CoA transporter, 26
ABC-type Fe³⁺ transporter, 9
ABC-type ferric citrate transporter, 12
ABC-type ferric enterobactin transporter, 12
ABC-type ferric hydroxamate transporter, 11
ABC-type glutathione transporter, 20
ABC-type glutathione-S-conjugate transporter, 26
ABC-type glycerol 3-phosphate transporter, 28
ABC-type guanine transporter, 27
ABC-type heme transporter, 26
ABC-type lipid A-core oligosaccharide transporter, 23
ABC-type lipopolysaccharide transporter, 23
ABC-type maltose transporter, 22
ABC-type methionine transporter, 20
ABC-type Mn²⁺ transporter, 9
ABC-type molybdate transporter, 17
ABC-type Na⁺ transporter, 8
ABC-type Ni²⁺ transporter, 10
ABC-type nitrate transporter, 16
ABC-type nonpolar-amino-acid transporter, 18
ABC-type oligopeptide transporter, 19
ABC-type oligosaccharide transporter, 22
ABC-type phosphate transporter, 15
ABC-type phosphonate transporter, 16
ABC-type polar-amino-acid transporter, 18
ABC-type polyamine transporter, 28
ABC-type putrescine transporter, 29
ABC-type quaternary amine transporter, 28
ABC-type sulfate transporter, 16
ABC-type taurine transporter, 27
ABC-type teichoic-acid transporter, 22
ABC-type thiamine transporter, 29
ABC-type tungstate transporter, 17
ABC-type tyrosine transporter, 21
ABC-type vitamin B₁₂ transporter, 27
ABC-type xenobiotic transporter, 26
ABC-type Zn²⁺ transporter, 12
arsenite-transporting ATPase, 17
ascorbate ferrireductase (transmembrane), 7
bacterial ABC-type protein transporter, 19
biotin-dependent malonate decarboxylase, 14
caldariellaquinol oxidase (H⁺-transporting), 2
carboxybiotin decarboxylase, 13
Cd²⁺-exporting ATPase, 13
chloroplast protein-transporting ATPase, 18
cytochrome-*c* oxidase, 4
ferredoxin—NAD⁺ oxidoreductase (H⁺-transporting), 5
ferredoxin—NAD⁺ oxidoreductase (Na⁺-transporting), 7
ferredoxin—quinone oxidoreductase (H⁺-translocating), 4
glutaconyl-CoA decarboxylase, 15
H⁺-exporting diphosphatase, 6
H⁺-transporting two-sector ATPase, 6
H⁺/K⁺-exchanging ATPase, 12
menaquinol oxidase (H⁺-transporting), 3
(*S*)-methylmalonyl-CoA decarboxylase (sodium-transporting), 14
mitochondrial protein-transporting ATPase, 18
Na⁺-exporting diphosphatase, 13
Na⁺-transporting two-sector ATPase, 7
Na⁺/K⁺-exchanging ATPase, 11
NADH:ubiquinone reductase (H⁺-translocating), 2
NADH:ubiquinone reductase (Na⁺-transporting), 7
oxaloacetate decarboxylase (Na⁺ extruding), 14
P-type Ag⁺ transporter, 11
P-type Ca²⁺ transporter, 10
P-type Cu⁺ transporter, 9
P-type Cu²⁺ transporter, 10
P-type H⁺-exporting transporter, 6
P-type K⁺ transporter, 9
P-type Mg²⁺ transporter, 11
P-type Mn²⁺ transporter, 13
P-type Na⁺ transporter, 8
P-type phospholipid transporter, 25
P-type Zn²⁺ transporter, 10
plastoquinol—plastocyanin reductase, 3
protein-secreting ATPase, 19
proton-translocating NAD(P)⁺ transhydrogenase, 1
quinol oxidase (electrogenic, proton-motive force generating), 3
quinol—cytochrome-*c* reductase, 4
succinate dehydrogenase (electrogenic, proton-motive force generating), 5
ubiquinol oxidase (H⁺-transporting), 2