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Dissimilation of C₃-sulfonates

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Abstract Cysteate and sulfolactate are widespread natural products in the environment, while propane-sulfonate, 3-aminopropanesulfonate and propane-1,3-disulfonate are xenobiotics. While some understanding of the bacterial assimilation of cysteate sulfur has been achieved, details of the dissimilation of cysteate and sulfolactate by microbes together with information on the degradation of the xenobiotics have only recently become available. This minireview centres on bacterial catabolism of the carbon moiety in these C₃-sulfonates and on the fate of the sulfonate group. Three mechanisms of desulfonation have been established. Firstly, cysteate is converted via sulfofpyruvate to sulfolactate, which is desulfonated to pyruvate and sulfite; the latter is oxidized to sulfate by a sulfite dehydrogenase and excreted as sulfate in *Paracoccus pantotrophus* NKN-CYSA. Secondly, sulfolactate can be converted to cysteate, which is cleaved in a pyridoxal 5'-phosphate-coupled reaction to pyruvate, sulfite and ammonium ions; in *Silicibacter pomeroyi* DSS-3, the sulfite is excreted largely as sulfite. Both desulfonation reactions seem to be widespread. The third desulfonation mechanism is oxygenolysis of, e.g. propanesulfonate(s), about which less is known.

Keywords L-Cysteate · Desulfonation · Sulfite dehydrogenase · 3-Sulfolactate · 3-Sulfofpyruvate · Sulfate exporters · Sulfite exporters

Introduction

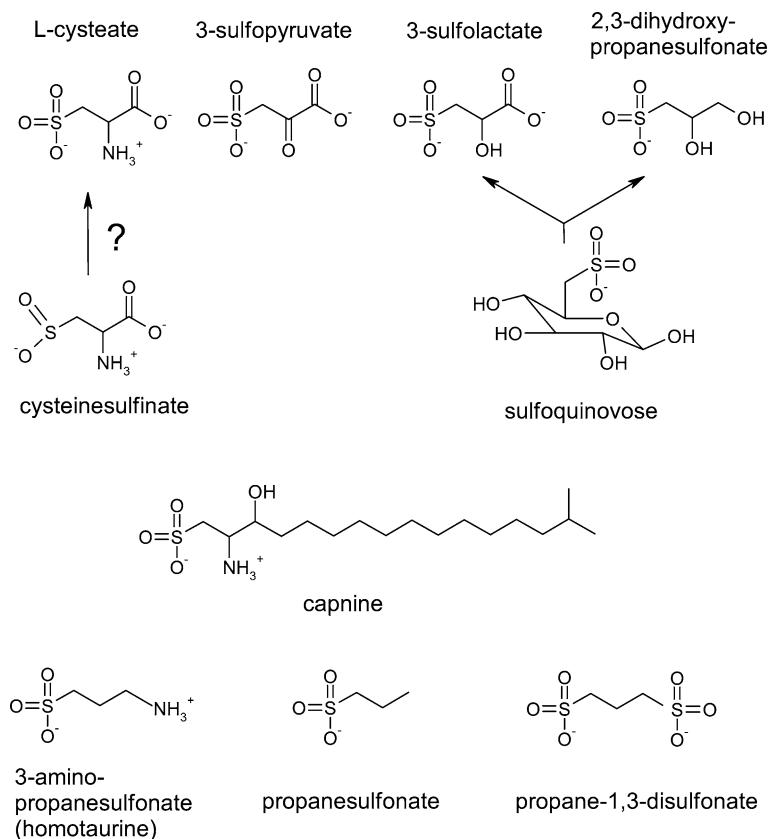
Organosulfonates are widespread compounds of natural and anthropogenic origin in air, soil and water (e.g. Cook and Denger 2002; Cook et al. 1999; Kelly and

Murrell 1999; Lie et al. 1998). The aliphatic sulfonates have aroused much interest in mammalian metabolism (e.g. Huxtable 1992; Stipanuk 2004): their lower profile in microbial metabolism may change when the significance of the high frequency of occurrence of the relevant degradative genes in the metagenome of the Sargasso Sea (our analyses of published data, Venter et al. 2004) is evaluated experimentally, and when the frequency with which the same genes are observed and incorrectly annotated in genome sequences is appreciated.

One group of these aliphatic sulfonates has received little attention, e.g. the C₃-sulfonates (Fig. 1). The most prominent C₃-sulfonate is probably L-cysteate (2-amino-3-sulfofpropionate), whose relevance to microbial metabolism is indicated by the fact that it is degraded immediately by microbial mats (Visscher et al. 1999). The compound was first discovered as weathered residues of cysteine in wool (Consden et al. 1946) and was believed to be a key intermediate in one biosynthetic pathway (e.g. Metzler 1977) of taurine (2-aminoethane-sulfonate), which is the major organic solute in mammals (Huxtable 1992). However, Huxtable (1992) and Stipanuk (2004) do not mention the 'cysteate' pathway, no cysteate is formed from L-cysteine if samples are correctly worked up (e.g. Bagley et al. 1995), and the proposed decarboxylative enzyme in the pathway, cysteine-sulfinate decarboxylase [EC 4.1.1.29], has a non-physiological *K_m* value for L-cysteate (e.g. Guion-Rain et al. 1975). The 'cysteate pathway' to taurine in mammals is, thus, an artefact: taurine is synthesized by an incompletely described set of enzymes via L-cysteine sulfinate and hypotaurine (e.g. Stipanuk 2004). The presence of L-cysteate on spiders' webs, with molar concentrations of taurine derivatives, was attributed to its role in taurine biosynthesis (Fischer and Brander 1960): even if the L-cysteate in these determinations were artefactual, cysteate is likely to be a weathering product of excreted L-cysteine sulfinate in situ, thus, widespread extracellular L-cysteate from this source can be predicted in the environment. L-cysteate is one educt in the biosynthesis of the cytophagal sulfolipid, capnine (Fig. 1)

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Fig. 1 Some naturally occurring and some commercially available C₃-organosulfonates. The natural products in the *top line*, and the xenobiotic compounds in the *bottom row* are mentioned in the text. While L-cysteate is formed spontaneously from L-cysteine sulfinic acid, there is no evidence to support biological catalysis of the reaction in mammals: the current authors now suspect that the reaction is catalyzed by some bacterial enzymes. The generation of, e.g. sulfolactate from sulfoquinovose, involves two sulfonated fructose derivatives and sulfolactaldehyde (Roy et al. 2003), so the range of even naturally occurring C₃-sulfonates in this figure is incomplete



(White 1984), of algal sulfolipids (Anderson et al. 1979) and possibly of another bacterial sulfolipid (Corcelli et al. 2004), thus, cysteate (or another C₃-sulfonate) can be anticipated as an intermediate in the degradation of these compounds. Two biotransformation products from (dietary) L-cysteate in mammals, 3-sulfo-pyruvate and 3-sulfolactate, are excretion forms (Weinstein and Griffith 1988). Another widespread source of 3-sulfolactate, presumably L-3-sulfolactate, is bacterial endospores (Bonsen et al. 1969; Graham and White 2002; Graham et al. 2002). Most recently, 3-sulfolactate has been detected as a minor excretion product during the bacterial dissimilation of sulfoquinovose, a component of the plant sulfolipid; larger amounts of 2,3-dihydroxypropanesulfonate are found as a transient intermediate during degradation (Roy et al. 2003). Homotaurine (3-aminopropanesulfonate) (AlzhemedTM, CerebrilTM) is a drug candidate for two major conditions (Alzheimer and stroke). The N-acetyl derivative of homotaurine (Campral®) is used to treat alcoholics (Scott et al. 2005), while as a quaternary amine(s) it functions as an amphoteric surfactant (e.g. CHAPS), thus, homotaurine can be expected in sewage works. Propanesulfonate can be used in mobile phases for HPLC. Propane 1,3-disulfonate is another drug candidate (FibrillexTM).

Until recently, there was little information on the biochemistry of the microbial degradation of C₃-sulfoxides (in contrast to the assimilation of cysteine-sulfur (Eichhorn and Leisinger 2001; Kertesz 2000)), and no

gene encoding an enzyme, transporter or regulator was known. This situation has altered significantly.

Growth with C₃ sulfonates

L-Cysteate was first observed to be a sole source of carbon and energy for bacteria under aerobic conditions (Stapley and Starkey 1970): the authors firstly observed extensive deamination, which usually preceded desulfonation, and then transient release of sulfite, which was converted to sulfate. L-Cysteate was later found to serve as an electron acceptor for several sulfate- or sulfite-reducing bacteria (Laue et al. 1997b; Lie et al. 1996, 1998, 1999): the fate of the cysteate carbon is largely acetate, and the sulfonate sulfur is recovered as sulfide. L-Cysteate can serve as an electron donor for some nitrate-reducing bacteria (Denger et al. 1997; Mikosch et al. 1999). *Paracoccus pantotrophus* NKNCYSA grows exponentially with L-cysteate as the electron donor and nitrate as the electron acceptor, and excretes the sulfonate moiety as sulfate; the amino group is recovered largely as ammonium ion in the medium and in part in cell material (Mikosch et al. 1999). The organism grows equally well under oxic conditions (Rein et al. 2005). Corresponding to the oxidation or reduction of cysteate, the compound can be dismutated in a fermentation (Laue et al. 1997a). Here again, exponential growth with quantitative substrate utilization and generation of

acetate is observed; not only the substrate, but also the sulfite from desulfonation (Figs. 3, 4) is dismutated, to sulfide and sulfate (Laue et al. 1997a). Less information is available on the utilization of sulfolactate or sulfo-pyruvate. Sulfolactate has now been found to serve as a sole source of carbon and energy for the aerobic growth of *P. pantotrophus* NKNCYSA, *Cupriavidus necator* JMP134 and *Silicibacter pomeroyi* DSS-3^T (Denger et al. 2006; Rein et al. 2005) and as an electron acceptor for the strictly anaerobic, sulfite-reducing *Desulfotobacterium hafniense* DCB-2 (Rein et al. 2005). L-Cysteine-sulfinate, whose biological conversion to cysteate in mammals has been disproven (see Introduction) is a growth substrate for *S. pomeroyi* DSS-3 (Denger et al. 2006).

Propanesulfonate is a sole source of carbon and energy for the strict aerobe *Comamonas acidovorans* P53; the sulfite generated on desulfonation is excreted as sulfate (Reichenbecher et al. 1999). Propane-1,3-disulfonate is utilized as a sole source of carbon and energy by *Ralstonia* sp. strain EDS1; here again, the sulfonate moiety is recovered as sulfate (Denger and Cook 2001). Utilization of homotaurine as a sole source of carbon or of nitrogen for growth has recently been detected in this laboratory (J. Mayer et al., unpublished).

Transporters, enzymes and genes

A lack of information on transport

It is axiomatic that ionic organosulfonates require transport systems to cross the cell membrane (Graham et al. 2002). There are, as yet, no data on transporters involved in the dissimilation of a C₃-sulfonate. However, Eichhorn et al. (2000) have shown that the ATP binding cassette transporter, SsuABC, is involved in the uptake of propanesulfonate in *Escherichia coli*, for which the compound serves as a sole source of sulfur. 3-Amino-propanesulfonate is a substrate for the SsuABC and TauABC transporter systems, and evidence for the presence of further transporters was obtained (Eichhorn et al. 2000). The involvement of energy-dependent pumps to transport C₃-sulfonates into the cell prior to dissimilation is suspected, as indicated for the C₂-sulfonates (Cook and Denger 2005).

The desulfonation of L-cysteate via sulfolactate

The overall deamination of L-cysteate in *P. pantotrophus* NKNCYSA (Fig. 2a), comprising transaminase and L-glutamate dehydrogenase [EC 1.4.1.4], is constitutive (Mikosch et al. 1999; Rein et al. 2005), and it is postulated (Rein et al. 2005) that the transaminase could be L-aspartate transaminase [EC 2.6.1.1], which can catalyze the transamination of L-cysteate in mammalian tissue (Weinstein and Griffith 1988). The reduction of 3-sulfo-pyruvate to 3-sulfolactate is also catalyzed by a constitutive enzyme, and Rein et al. (2005) consider it

likely that, as in mammals, the reaction is catalyzed by L-malate dehydrogenase [EC 1.1.1.37]. These hypotheses await testing.

The inducible portion of the pathway is the desulfonative enzyme, 3-sulfolactate sulfo-lyase (SuyAB) [EC 4.4.1.-]. The reaction is stoichiometric, and the enzyme appears to contain a tightly bound iron atom, whose presence was suspected, when it became clear from the deduced amino acid sequence that the enzyme has similarities to the Fe²⁺-dependent altronate dehydratases (Rein et al. 2005). The enzyme is soluble and it contains two subunits, α and β , which have molecular masses of 8 and 42 kDa, respectively. SuyAB represents about 10% of the soluble protein in the induced cell, both in *P. pantotrophus* NKNCYSA and in *C. necator* JMP134, where the authors predicted its presence from the genome sequence: which of the four sets of candidate genes encodes SuyAB in strain JMP134 is still unclear (Rein et al. 2005).

The discussion of the desulfonation of 3-sulfolactate has avoided one significant problem, the chirality of the compound. Growth involved the use of racemic 3-sulfolactate, and both optical isomers were utilized by, e.g. *P. pantotrophus* NKNCYSA and *C. necator* JMP134, as judged by the growth yield and the sulfate recovery. The crude enzyme preparation from *P. pantotrophus* NKNCYSA converted about 50% of the substrate to pyruvate rapidly, also when a second portion of substrate was added, and the remainder slowly. This was interpreted to represent the activity of a 3-sulfolactate racemase. Presumably, there are two stereo-specific transporters for sulfolactate (where only one is shown in Fig. 2a, b), and a racemase (not shown in Fig. 2a, b) to allow both stereoisomers of sulfolactate to be degraded.

Three genes, *suyAB* and the downstream gene, *suyZ*, seem to represent an operon (RT-PCR) (Rein et al. 2005). Those authors consider that SuyZ, deduced to be a membrane protein with a maximum of ten trans-membrane helices, must have the same value to the cell as the desulfonation reaction, which releases the carbon atoms as pyruvate for growth. The function they hypothesize is excretion of the sulfur oxyanion, in order to maintain constant osmotic pressure in the cell. *P. pantotrophus* NKNCYSA contains an inducible sulfite dehydrogenase, and excretes only sulfate. So SuyZ is a putative channel to export sulfate (Rein et al. 2005).

Deamination of L-cysteate preceded desulfonation in early work (Stapley and Starkey 1970), whereas e.g. Mikosch et al. (1999) observed substrate utilization and formation of both products to be concomitant. The earlier work presumably involved transient excretion of sulfolactate as an explanation of the phased appearance of ammonium and sulfate. Phased appearance of these products could scarcely occur when one enzymic reaction releases both inorganic products simultaneously (Fig. 2b, see subsequent paragraph) and transient excretion of a sulfonate has been observed recently (Roy et al. 2003). This hypothesis of transient excretion requires both an exporter and an uptake system for

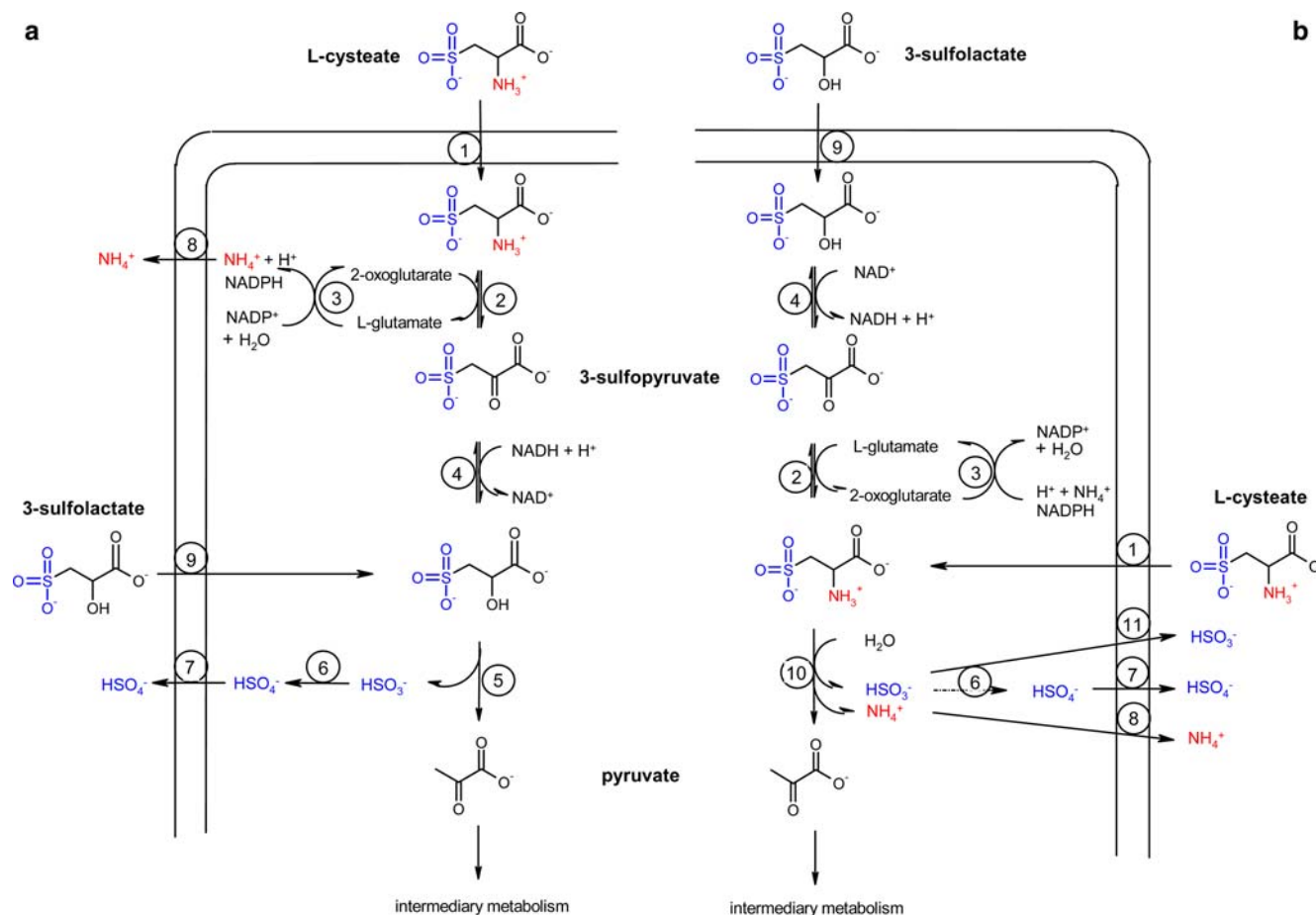


Fig. 2 Desulfonation of L-cysteate via sulfolactate in *P. pantotrophus* NKNCYSA (a), contrasted with the direct desulfonation of L-cysteate in *S. pomeroiy* DSS-3 (b). Each organism can utilize sulfolactate (Denger et al. 2006; Rein et al. 2005). The numbered reactions are: (1), uptake of L-cysteate; (2), L-cysteate:2-oxoglutarate aminotransferase; (3), L-glutamate dehydrogenase; (4), 3-(L)-sulfolactate dehydrogenase; (5), 3-(L)-sulfolactate sulfo-lyase; (6), sulfite dehydrogenase; (7), sulfate exporter; (8), ammonium

exporter; (9), uptake of 3-sulfolactate; (10), L-cysteate sulfo-lyase (deaminating); (11), sulfite exporter. The published pathway in (b) has been extended to include constitutive 3-sulfolactate dehydrogenase (possibly L-malate dehydrogenase, SPO0349), L-cysteate:2-oxoglutarate aminotransferase (possibly L-aspartate aminotransferase, SPO1264) and L-glutamate dehydrogenase (presumably SPO1743) (K. Denger, unpublished)

3-sulfolactate. Exporters of organosulfonates have been deduced in taurine metabolism, when the compound is utilized as a source of nitrogen (Cook and Denger 2005), and general evidence for the uptake system is the utilization of the compound as a carbon source by *P. pantotrophus* NKNCYSA (Fig. 2) and other organisms (Denger et al. 2006; Rein et al. 2005).

The direct desulfonation of cysteate

Rein et al. (2005) noted that their pathway (Fig. 2a) was not representative for most of their collection of L-cysteate-dissimilating bacteria. *S. pomeroiy* DSS-3 was reported to utilize cysteate (González et al. 2003), but the genome (Moran et al. 2004) does not contain *suyAB*-like genes, though it does contain a *suyZ*-like gene (SPOA0157). Denger et al. (2006) hypothesized that SPOA0158, annotated to encode D-cysteine desulfhydrase, a pyridoxal 5'-phosphate-coupled enzyme, would

encode L-cysteate sulfo-lyase (deaminating) (CuyA) (Figs. 2b, 3). They detected the inducible activity in *S. pomeroiy* DSS-3, *Bilophila wadsworthia* RZATAU and other bacteria, and confirmed their hypothesis by purifying the enzyme and confirming CuyA to be SPOA0158. The *cuyAZ*-genes were cotranscribed and hypothesized to be regulated by the LysR-type product of the neighbouring gene, SPOA0159.

CuyA is homomultimeric and catalyzes not only the L-cysteate sulfo-lyase reaction but also, at a lower rate, the D-cysteine desulfhydrase reaction. L-Cysteine sulfinate is not a substrate for the enzyme. The named reaction of this COG group (COG 2515), 1-aminocyclopropane-1-carboxylate deaminase, is not catalyzed (Denger et al. 2006).

B. wadsworthia RZATAU and some other organisms utilize racemic 3-sulfolactate quantitatively. *S. pomeroiy* DSS-3 utilizes 3-sulfolactate poorly (about 10% recovery of sulfate) (Denger et al. 2006); correspondingly,

activities of a sulfolactate dehydrogenase (e.g. L-malate dehydrogenase), L-cysteate:2-oxoglutarate aminotransferase and L-glutamate dehydrogenase (Fig. 2b) were detected in cell extracts of strain DSS-3 (K. Denger, unpublished). When strain DSS-3 utilizes L-cysteine sulfinate, cell extracts were found to be fully induced for L-cysteate sulfo-lyase (K. Denger, unpublished). L-Cysteate could thus be a point of convergence of catabolism of different C₃-sulfonates in *S. pomeroyi* DSS-3.

Oxygenolytic desulfonation

Most organosulfonates share the property of stability, but compounds like cysteate contain substituents, which allow the C-sulfonate bond to be destabilized and cleaved (Figs. 2, 3). Compounds like propanesulfonate (Fig. 4) lack these substituents and require less subtle methods to cleave the C-sulfonate bond, oxygenation. Reichenbecher et al. (1999) present evidence which suggests that a soluble, multi-component monooxygenase converts propanesulfonate to propanal in the first metabolic step in the degradative pathway in *C. acidovorans* P53. The suggested structure in Fig. 4 is derived from work with the more stable methanesulfonate monooxygenase (Baxter et al. 2002; Kelly and Murrell 1999). Propanesulfonate monooxygenase has a broad substrate spectrum for the alkyl group, but the one disulfonate tested was not a substrate. The current authors suspect that similar enzymes of different specificity are involved in the two desulfonation steps needed by *Ralstonia* sp. strains EDS1 or EDS2 when they utilize

propane-1,3-disulfonate (Fig. 4) (Denger and Cook 2001). It is further hypothesized that a transaminase (or a dehydrogenase) could attack homotaurine and make propanal-3-sulfonate a point of convergence in the degradation of C₃-sulfonates (Fig. 4).

Fates of the ammonium ion

About 20% of the ammonium ion released during growth with L-cysteate is assimilated into cell polymers (e.g. Denger et al. 2006; Laue et al. 1997a; Mikosch et al. 1999). The residual ammonium ion is excreted during growth (Fig. 2), as it has been known for over a century in the dissimilation of amino acids. This phenomenon does not seem to have been explained at the molecular level, but Amt (ammonium-methylammonium transport) proteins may be involved (Booth et al. 2005; Khademi et al. 2004; A. Gorzynska and Smits, unpublished).

Fates of the sulfite ion

Sulfite is the direct product of enzymic desulfonation (Figs. 2, 3, 4), but this anion itself is seldom excreted in large amounts into the medium. The known exceptions involve *S. pomeroyi* DSS-3 and *Paracoccus versutus* N-MT (Denger et al. 2006; S. Weinitschke et al., submitted). The current authors suspect that in these organisms, a sulfite exporter is present, whose affinity for sulfite exceeds that of the sulfite dehydrogenase [EC 1.8.2.1], which is also present (Denger et al. 2006). It is normal for aerobes to involve a sulfite dehydrogenase to

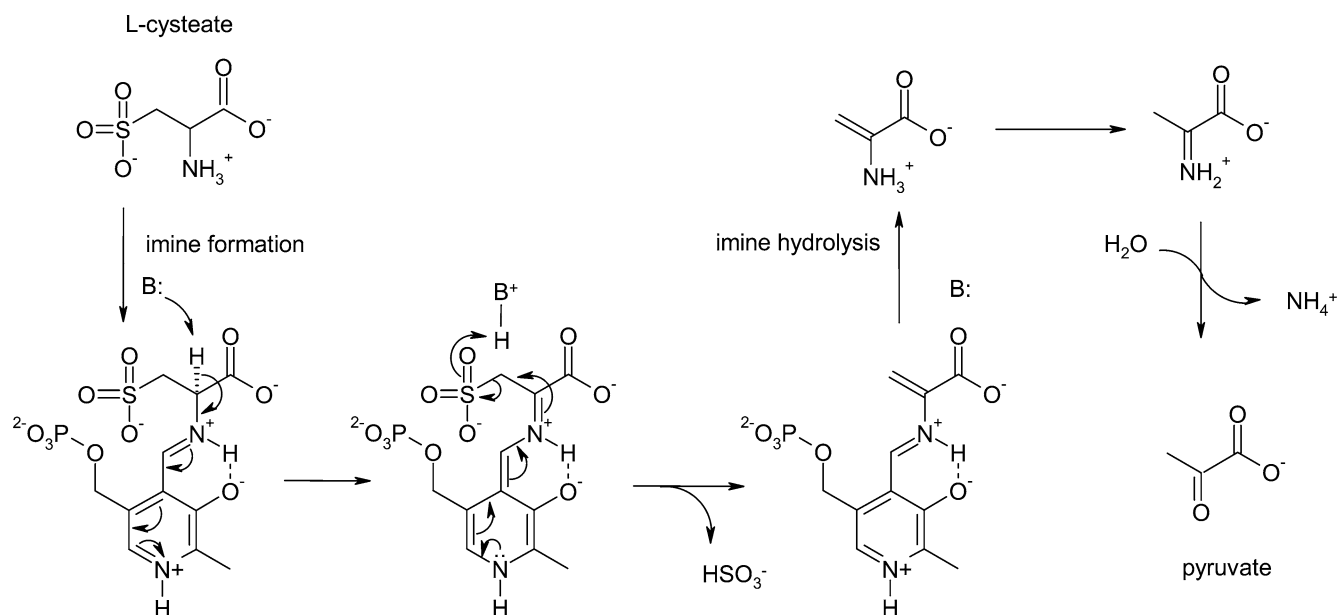


Fig. 3 Presumed mechanism of L-cysteate sulfo-lyase from *Silicibacter pomeroyi* DSS-3. The term 'imine formation' covers the presumed transimination from a lysyl residue (possibly K293) to the cysteate-imine shown. The flow of electrons through the

pyridoxal 5'-phosphate co-factor and the β -elimination are adapted from a standard text, which suggests that the deamination reaction subsequent to the 'transimination' of the co-factor to the lysyl group on the enzyme is enzymatic (Metzler 2003)

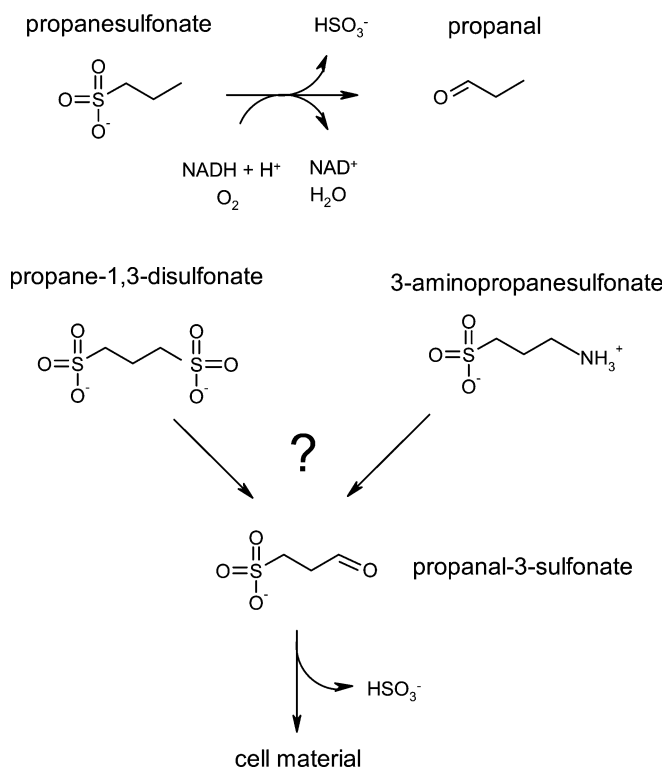


Fig. 4 Known and predicted reactions required to desulfonate derivatives of propanesulfonate. While the desulfonation of propanesulfonate has been observed in cell extracts, the pathways for homotaurine and 1,3-disulfopropane are hypotheses, based on the facts that growth experiments are in mass balance

detoxify sulfite to sulfate, which is believed to be removed from the cell by one of several putative sulfate exporters (Cook and Denger 2005; Rein et al. 2005). There would appear to be no reports of sulfite oxidase [EC 1.8.3.1] in bacteria (Cook and Denger 2005). There are, however, several different sulfite dehydrogenases [EC 1.8.2.1], but only one has been characterized, the cytochrome-*c*-coupled sulfite oxido-reductase (SorAB) from *Starkeya novella* (Kappler et al. 2000; Kappler and Dahl 2001). The enzyme is periplasmic; SorA is a molybdenum cofactor-containing dehydrogenase and SorB is a cytochrome *c*. Homologues of the *sorAB* genes are only now being found to be widespread in genome sequences. Single *sorA*-like genes (*suox*, sulfite oxidation) without a *sorB* (as neighbour) are also widespread. These SorA- and Suox-sequences share some sequence similarity with SoxC sequences in the autotrophic sulfur oxidation pathway. The ferricyanide-linked sulfite dehydrogenase discovered by Reichenbecher et al. (1999) in *C. acidovorans* P53, observed also in *S. pomeroyi* DSS-3 and *P. versutus* N-MT (Denger et al. 2006) and suspected in *Rhodobacter sphaeroides* 2.4.1 (K. Denger, unpublished), is independent of cytochrome *c*. There is no *sorA*-like gene (apart from *soxC*) in either *S. pomeroyi* DSS-3 or *R. sphaeroides* 2.4.1, so a novel sulfite dehydrogenase is awaiting characterization at the enzymatic and genetic level. In strict anaerobes, sulfite from cysteate can be dismutated into sulfate and sulfide or

reduced into sulfide, but only the latter reaction, in *B. wadsworthia* RZATAU, has been explored at the protein level (Cook and Denger 2002). More work is needed on this wide range of enzymes.

Exporters of sulfate and sulfite

The different forms of inorganic sulfur derived from sulfite are all recovered extracellularly. There are hypotheses, which identify some of the genes encoding the exporters of sulfate and sulfite: these genes are transcribed inducibly (Denger et al. 2006; Rein et al. 2005), but no exporter function has been confirmed biochemically. We presume that there are exporters for several organic sulfonates (e.g. Cook and Denger 2005; Roy et al. 2003) but clues to their identity are few.

Regulation

There is no information on this topic, although the pathways are inducible, and a putative regulator for the induction of cysteate sulfo-lyase in *S. pomeroyi* DSS-3 has been proposed (Denger et al. 2006). It is clear that the induction of the desulfonation reaction is independent of the induction of the sulfite dehydrogenase, whether the latter is cytochrome *c*-coupled or whether the artificial electron acceptor ferricyanide is needed. In both *S. pomeroyi* DSS-3 and *P. pantotrophus* NKN-CYSA, the sulfite dehydrogenase is induced when sulfite is released (L-cysteate or taurine as sole carbon sources), whereas each desulfonation reaction is specifically induced by the sulfonate present in the growth medium (Denger et al. 2006; Rein et al. 2005).

Conclusions

L-Cysteate, sulfo-pyruvate, sulfolactate and, presumably, 2,3-dihydroxypropanesulfonate (Fig. 1) are widespread in nature and subject to biodegradation. There are two established mechanisms of desulfonation in the dissimilation of these C_3 -sulfonates: (1) in the pathway from cysteate to sulfolactate via sulfolactate sulfo-lyase (Fig. 2a), and (2) in the pathway from sulfolactate to L-cysteate via L-cysteate sulfo-lyase (Fig. 2b). The largely xenobiotic alkylsulfonates seem to be subject to oxygenolytic desulfonation, where direct evidence for one multi-component, NADH-coupled monooxygenase is available; more such enzymes are likely. This initial understanding of the pathways, and potential access to genomic data (for the dissimilation of natural products), should allow the other aspects of the catabolism of sulfonates to be explored: transport into the cell, excretion of ammonium (if appropriate), sulfite dehydrogenases or sulfite reductases (as appropriate), excretion of sulfite and sulfate, and regulatory circuits for the desulfonation pathways and for the sulfite dehydrogenases.

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