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Isethionate as a product from taurine during nitrogen-limited growth of *Klebsiella oxytoca* TauN1

Abstract *Klebsiella oxytoca* TauN1 represents a group of isolates which utilise taurine (2-aminoethanesulfonate) quantitatively as a sole source of combined nitrogen for aerobic growth. During growth, a compound is excreted, which has now been identified as isethionate (2-hydroxyethanesulfonate). An ion-chromatographic separation of isethionate was developed to quantify the putative isethionate, whose identity was confirmed by matrix-assisted, laser-desorption ionisation time-of-flight mass spectrometry. Strain TauN1 utilised taurine (and excreted isethionate) concomitantly with growth. Cell-free extracts contained inducible taurine transaminase, which yielded sulfoacetaldehyde. A soluble, NADP-dependent isethionate dehydrogenase converted sulfoacetaldehyde to isethionate. The enzyme was partially purified and it apparently belonged to the family of short-chain alcohol dehydrogenases.

Keywords Isethionate formation · Taurine transaminase · Isethionate dehydrogenase · *Klebsiella oxytoca*

Introduction

Isethionate (2-hydroxyethanesulfonate, Fig. 1) was found initially as the major anion in the giant axon of the squid (Koechlin 1954), and it is widespread in cephalopods (Hoskin and Brandle 1973). It is a normal component of tissue of higher animals (e.g. Fellman et al. 1980; Kumpulainen et al. 1982), and is one excretion form of sulfonates from mammals and fungi (Braun and Fromageot 1962; Jacobsen et al. 1967). The source of mammalian isethionate has not yet been resolved. The compound has been attributed both to bacterial action on taurine (2-aminoethanesulfonate) in the gut (e.g. Fellman et al. 1980), and to purely eukaryotic reactions from taurine (Cunningham and Tipton 2000). One reason for this uncertainty is probably the lack of a simple assay for isethionate (e.g. Remtulla et al. 1977; Fellman et al. 1980). Isethionate is also found in large amounts in some red algae (Barrow et al. 1993; Holst et al. 1994) and on spider webs (Vollrath et al. 1990). Somewhat less natural, but very widespread, is the use of derivatised isethionates in hair shampoos and soap replacements for personal care (e.g. Sun et al. 2003), and isethionate is a counter-ion in pharmaceuticals (e.g. O'Neil 2001; Delobel and Pradinaud 2003). Corresponding to this widespread occurrence, many metabolic fates of isethionate are known in bacteria (Cook and Denger 2002), but no biochemical reaction with isethionate was understood until a dissimilatory, membrane-bound, cytochrome *c*-coupled isethionate dehydrogenase [EC 1.1.2.-] was discovered in *Paracoccus denitrificans* NKNIS (Brüggemann et al. 2004).

Taurine, the major organic solute in mammals (Huxtable 1992), also has many metabolic fates in bacteria (Cook and Denger 2002). Dissimilation of the carbon atoms involves sulfoacetaldehyde and sulfoacetaldehyde acetyltransferase (Xsc) [EC 2.3.3.15] in aerobic and anaerobic bacteria, whereas the assimilation of sulfonate sulfur follows the reaction of Xsc in anaerobes or of taurine dioxygenase [EC 1.14.11.17] in aerobes (Kertesz 2000; Cook and Denger 2002). Two different microbial reactions are known to generate sulfoacetaldehyde from taurine, the combination of taurine:pyruvate aminotransferase (Tpa) [EC 2.6.1.77] and alanine dehydrogenase (Ald) [EC 1.4.1.4] in, e.g. *Pseudomonas aeruginosa*, *Rhodococcus opacus* ISO-5 and *Bilophila wadsworthia* (Shimamoto and Berk 1980; Cook and Denger 2002; Denger et al. 2004a), or the oxidative

We hope that the Leader of the Sulfur Department, Norbert Pfennig LSD, will be amused by the biology involving some of the compounds from his domain.

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deamination via taurine dehydrogenase (presumably TauXY, [EC 1.4.2.-]) in e.g. *P. denitrificans* NKNIS (Kondo and Ishimoto 1987; Cook and Denger 2002; Ruff et al. 2003; Brüggemann et al. 2004).

More recently, taurine has been explored as a sole source of combined nitrogen for growth, a process previously followed simultaneously with the degradation of the compound as a source of carbon and energy (e.g. Chien et al. 1999). *R. opacus* ISO-5 utilises taurine-nitrogen in the presence of the carbon source glucose and induces the complete dissimilatory pathway for taurine, including Xsc, though regulated to a lower level of expression (Denger et al. 2004a): *R. opacus* thus releases the sulfonate-sulfur as sulfate. *Rhodopseudomonas palustris*, whose genome potentially encodes a taurine regulator and TauXY but contains no *xsc* gene (Brüggemann et al. 2004), does indeed utilise taurine as a sole source of combined nitrogen, and the sulfonate-sulfur is recovered quantitatively as sulfoacetate (Denger et al. 2004b).

We wondered whether the excretion of sulfoacetate was common, so we did enrichment cultures to obtain organisms able to utilise taurine as sole source of nitrogen for growth, and we isolated bacteria (Weinitschke et al. 2005). Most organisms excreted an organosulfonate, but none excreted sulfoacetate. One of these organosulfonates was identified as sulfoacetaldehyde, which was excreted by several organisms, mainly *Acinetobacter* spp. (Weinitschke et al. 2005). Other organisms, largely strains of *Klebsiella oxytoca*, were believed to release isethionate (Fig. 1). We now report that a representative isolate, *K. oxytoca* TauN1, transaminates taurine to sulfoacetaldehyde, which is reduced to isethionate by a soluble, NADP-coupled dehydrogenase and excreted.

Fig. 1 Pathway of assimilatory deamination of taurine-nitrogen by *Klebsiella oxytoca* TauN1. It is axiomatic that sulfonates require transport into the cell (Graham et al. 2002), and we presume that either an ATP-binding cassette or a tripartite ATP-independent system (*I*) is involved in transporting taurine into the cell (Kertesz 2001; Brüggemann et al. 2004). Evidence is provided in the text for the presence of taurine:pyruvate aminotransferase (*II*), alanine dehydrogenase (*III*) and isethionate dehydrogenase (*IV*). The isethionate exporter (*V*) is hypothesised, because the cell membrane is impermeable to sulfonates

Materials and methods

Organism, growth media and growth conditions

K. oxytoca TauN1 (DSM 16963) (Weinitschke et al. 2005) was used; the organism is classified as a group L2 pathogen and may not be grown in large volumes in our laboratory. The growth medium was a 50 mM potassium phosphate buffer, pH 7.2, which contained 0.25 mM $MgSO_4$, 10 mM succinate, 2 mM taurine (or ammonium ion in controls) and trace elements (Thurnheer et al. 1986). Growth was followed in 50-ml cultures in 300-ml Erlenmeyer flasks shaken in a water bath at 30°C. Samples (2 ml) were taken at intervals to measure turbidity and to determine the concentrations of protein, taurine and other organosulfonates, and the ammonium and sulfate ions. When larger amounts of cells were required for enzyme assays, 200-ml cultures in 1-l Erlenmeyer flasks were used. Rupture of harvested cells of *K. oxytoca* in a French pressure cell was as described for *A. calcoaceticus* (Weinitschke et al. 2005).

P. denitrificans NKNIS (DSM 15418) was also used. Extracts of the organism served as a positive control for TauXY (Brüggemann et al. 2004). Extracts of *R. opacus* ISO-5 (DSM 44600) were used as positive controls for the assay of Tpa and of Ald.

Analytical methods

Growth was followed as turbidity ($OD_{580} = 1.0 =$ 197 mg protein l^{-1}) and quantified as protein in a Lowry-type reaction with bovine serum albumin as the standard (Cook and Hütter 1981). Protein in crude extracts was assayed by protein-dye binding (Bradford 1976). Taurine was derivatised, separated and quantified by reversed-phase HPLC (Laue et al. 1997). Sulfate was determined turbidimetrically as a suspension of $BaSO_4$ (Sörbo 1987). Ammonium ion was determined by the Berthelot reaction (Gesellschaft Deutscher Chemiker 1996). The identity of isethionate was confirmed by matrix-assisted, laser-desorption ionisation time-of-flight mass spectrometry (MALDI-TOF-MS) in the negative ion mode with a matrix of 4-hydroxy-α-cyanocinnamic acid; these determinations were done under contract by K. Hollemeyer, Technical Biochemistry, Saarland University, Saarbrücken (e.g. Tholey et al. 2002).

Isethionate was determined by ion chromatography with chemical suppression and conductivity detection. The column was an anion exchanger (3AS; Sykam, Fürstenfeldbruck, Germany), which was maintained at 40°C. The mobile phase was 10% acetonitrile in 5 mM Na_2CO_3 and contained 0.005% 4-hydroxybenzonitrile. The flow rate was 1.8 ml min^{-1}. Samples (20 µl) were loaded by autosampler, and the retention time was 1.40 min. The standard curve was linear to at least 2.5 mM in growth medium ($R^2 = 0.99$, $n = 6$). Under these conditions, acetate eluted at 1.14 min and chloride at 1.67 min, so the growth medium should not have acetate as the carbon source, or as a major metabolic product, and the salts solution should contain a minimum of chloride. The chloride in the trace elements solution was detectable but did not interfere; the sensitivity of the determination for isethionate was 40% of that for chloride.

Enzyme assays

Isethionate dehydrogenase was assayed photometrically at 365 nm with a 10-mm light path at about 25°C. The reaction mixture routinely contained in 1.0 ml: 100 µmol potassium phosphate buffer, pH 6.0; 400 nmol sulfoacetaldehyde (as the bisulfite adduct), 150 nmol NADPH and 5–100 µg protein, with which the reaction was started. The reaction was linear for at least 1 min. The molar extinction coefficient of NADPH was taken to be 3.4 mmol l^{-1} cm^{-1}. Simple plots of rate versus substrate concentration were generated, and hyperbolic curves were fitted to these raw data in Microcal Origin, version 6.0, software to derive values of apparent K_M (K_M^{app}) and V_{max} for each substrate.

TauXY was assayed photometrically with either cytochrome *c* or dichlorophenol indophenol as the electron acceptor, as described elsewhere (Brüggemann et al. 2004). Tpa was assayed discontinuously by following taurine disappearance and alanine formation (Denger et al. 2004a). Ald was assayed photometrically (Denger et al. 2004a).

Chemicals

Sulfoacetaldehyde, as the bisulfite adduct, was used; the material and its synthesis were described elsewhere (Denger et al. 2001). Phosphonoacetaldehyde, which was synthesised by H.B.F. Dixon (Cambridge), was kindly made available by J.P. Quinn (Belfast). NADPH (> 95%) was from Merck.

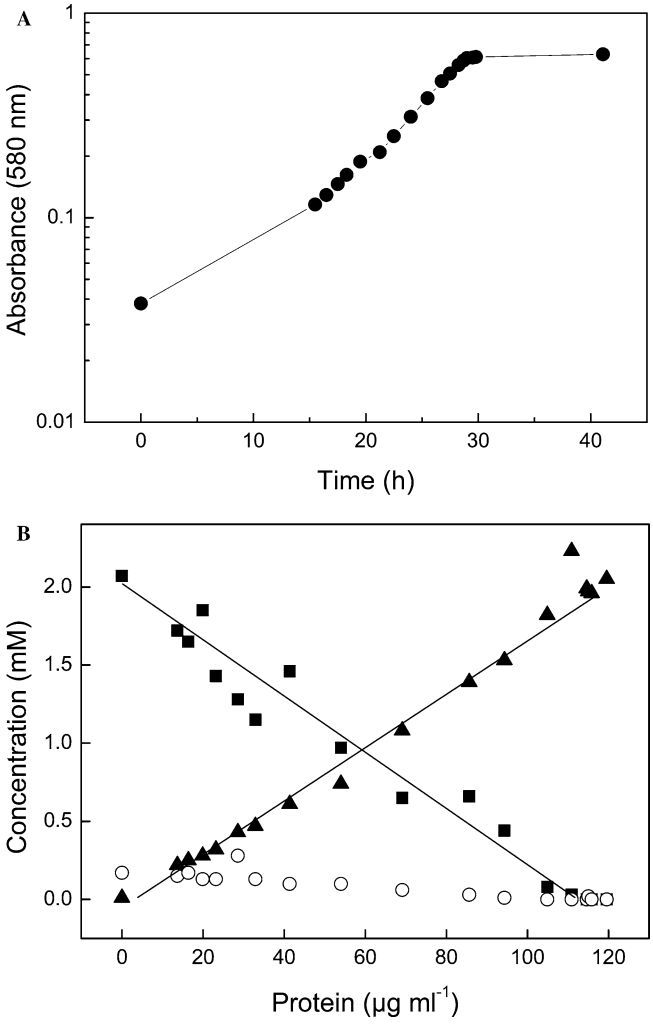

Fig. 2 A representative set of data on the growth of *K. oxytoca* TauN1 with taurine as the sole source of combined nitrogen in 10 mM succinate-salts medium. Growth was assayed as turbidity (**a**) and quantified as protein (**b**). *Filled circle* turbidity, *filled square* taurine, *filled triangle* isethionate, *open circle* ammonium ion

Results and discussion

Growth of *K. oxytoca* TauN1 with taurine and identification of the excreted isethionate

In a preliminary experiment with a set of small cultures of *K. oxytoca*, which initially contained 0–2.5 mM taurine as the source of nitrogen in 10 mM succinate-salts medium, we could confirm the disappearance of taurine by the end of growth and observe the formation of a compound which co-eluted from the ion chromatographic column with authentic isethionate. About 1 mol isethionate (mol taurine)$^{-1}$ was formed. No isethionate was formed during growth with the ammonium ion as the source of nitrogen. There was no growth under these conditions without a source of combined nitrogen.

Samples from the lag phase and from the stationary phase of growth of one of those cultures was examined by MALDI-TOF-MS in the negative ion mode. Taurine ($M_r = 125$), observed at the start of the experiment as a peak at $m/z = 124$ $[M-1]^-$, was absent at the end of growth, when a peak at $m/z = 125$ $[M-1]^-$ was detected. This represented isethionate ($M_r = 126$). Authentic samples of taurine and isethionate served as standards.

K. oxytoca TauN1 grew exponentially with taurine as the nitrogen source in succinate-salts medium (Fig. 2a). The specific growth rate (μ) was 0.13 h^{-1}. The utilisation of taurine was concomitant with growth, and the molar growth yield was about 58 g protein (mol N)$^{-1}$ (Fig. 2b), which corresponds to quantitative incorporation of the taurine-nitrogen into cell biomass (Cook 1987); a negligible amount on ammonium was detected transiently in the growth medium (Fig. 2b). The unit stoichiometry of release of isethionate, which was also concomitant with growth, was confirmed (Fig. 2b). The specific degradation rate of taurine during growth was derived from the specific growth rate and the growth yield as 0.6 mkat (kg protein)$^{-1}$.

Enzymes detected and the taurine transformation pathway in *K. oxytoca* TauN1

A deamination of taurine was predicted (Fig. 1), and assays for both TauXY and taurine transaminase were carried out with cell extracts. No TauXY was detected. In contrast, inducible Tpa was detected in extracts of taurine-grown cells. The specific activity was about 0.1 mkat (kg protein)$^{-1}$. Inducible Ald was also detected, but interference from NADH-oxidase prevented quantification. The specific activity of the transaminase was lower than the specific turnover rate in whole cells [0.6 mkat (kg protein)$^{-1}$], but no attempt was made to optimise the assay, as this was not the key reaction in this project.

Taurine-grown cells were found to contain a $NADP^+$-coupled isethionate dehydrogenase. There was no activity in extracts of ammonium-grown cells. The inducible enzyme was found in the supernatant fluid after ultracentrifugation, and the washed pellet of membranous material was inactive. This isethionate dehydrogenase is soluble, in contrast to the membrane-bound, cytochrome *c*-coupled enzyme involved in the dissimilation of taurine in *P. denitrificans* NKNIS (Brüggemann et al. 2004).

Soluble isethionate dehydrogenase was found to be active over a broad pH range. The optimum in citrate buffer was in the pH range of 5–6. The specific activity in phosphate-buffered crude extract showed a maximum [3 mkat (kg protein)$^{-1}$ at 30°C] at the extreme range of the buffer at pH 6.0. The temperature optimum was about 40°C, but enzyme activity could be detected readily at 50°C. The K_M^{app} value for NADPH was about 22 μM, that for sulfoacetaldehyde about 25 μM. There was thus sufficient enzyme activity in the cell to explain the growth rate; the affinity for NADPH indicates that the cofactor was present in saturating concentrations, if concentrations in other bacteria (0.2–0.4 mM) are relevant (e.g. Cook and Schlegel 1978), and the high affinity for sulfoacetaldehyde should prevent this compound accumulating, if it is toxic for the cell.

Two other potential substrates for the enzyme were tested in the separated enzyme (described in the following paragraph). Acetaldehyde was not reduced, but phosphonoacetaldehyde disappeared from the reaction mixture, which was accompanied by disappearance of NADPH.

Crude extracts (about 20 mg protein ml^{-1}) from taurine-grown cells of strain TauN1 were treated to remove the membranous material and DNA, after which, proteins were separated on an anion-exchange column. Isethionate dehydrogenase eluted with many other proteins at about 0.15 M Na_2SO_4. The pH of the sample was altered, and the concentrated fraction was subject to a second separation, which yielded a 50-fold purification of the enzyme with 20% yield. There were still five candidate proteins present (SDS-PAGE, not shown), but comparisons of different preparations allowed only a 29-kDa protein to be proposed as isethionate dehydrogenase. Activity was lost on hydrophobic interaction chromatography. The proteins were poorly separated with high loss by gel filtration, but native isethionate dehydrogenase appeared to have an M_r value of about 80 kDa, so the enzyme was presumed to be a multimer. The 29-kDa band of denatured protein was blotted on to a polyvinylidenefluoride membrane and yielded an N-terminal amino acid sequence, ATSKVVFITG, whose similarity to entries in the National Center for Biotechnology Information database supports the hypothesis that isethionate dehydrogenase is a member of the superfamily of short-chain dehydrogenases/reductases [EC 1.1.1.-] (e.g. Oppermann et al. 2001).

Significance of the findings

The ability to determine isethionate routinely in small portions of growth medium and in enzyme assays was the key to doing this work. Holst et al. (1994) needed 200-g portions of dry plant material, separations and then nuclear magnetic resonance and fast atom bombardment-MS analyses. Others needed sophisticated double-label technology (e.g. Fellman et al. 1980; Hoskin and Noonan 1980) and cited unreliable methods. The new method may allow some of the uncertainties in the literature to be answered conclusively.

The bacterial formation of isethionate from taurine was introduced by Fellman et al. (1980). The present work shows the transformation in pure culture to be quantitative (Fig. 2), and indicates some of the biochemistry involved (Fig. 1). The current observation (Fig. 2) is only one part of a larger phenomenon, whereby taurine, and seemingly only taurine, is often converted to a sulfonate rather than being oxidised to sulfate (Weinitschke et al. 2005). The isethionate exporter (Fig. 1) is the newest of a set of putative channels to excrete sulfur oxyanions or organosulfonates from bacteria (Brüggemann et al. 2004; Denger et al. 2004b; Rein et al. 2005; Weinitschke et al. 2005).

The formation of isethionate from taurine (Braun and Fromageot 1962), which was supplied as the sole source of sulfur for growth of *Aspergillus niger*, presumably resulted from supplying the nutrient in 100-fold excess. Presumably the reactions in Fig. 1 are present in this fungus also.

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