FERMENTATION OF AMINO ACIDS BY MICROCOCCUS AEROGENES

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The anaerobic micrococci described by Foubert and Douglas (1948a) may be divided into 3 groups on the basis of ability to degrade organic compounds: (1) those capable of fermenting only glycine (Douglas, 1951), (2) those able to degrade purines (Whiteley and Douglas, 1951) and many organic acids (Foubert and Douglas, 1948b), and (3) those able to ferment purines and a limited number of amino acids and organic acids. To the first group belong the species Micrococcus variabilis and Micrococcus anaerobius, to the second, Micrococcus lactilyticus (also called Veillonella gazogenes), and to the third, Micrococcus aero- genes, Micrococcus prevotii, Micrococcus activus, and Micrococcus acaccharolyticus. A survey of nine strains belonging to the third group has shown that serine, threonine, histidine, glutamic acid (and glutamine), pyruvate, α-ketobutyrate and urocanate are fermented. Although the strains vary considerably, each compound is degraded by at least one strain of each species, and all are fermented by strain 228 of M. aero- genes. The fermentation of purines by this strain has been described (Whiteley, 1952). This communication presents the results of studies on the fermentation of amino acids and a discussion of the mechanisms of degradation by M. aerogenes.

METHODS

Cells were grown either in the peptone-yeast extract medium ("peptone medium") described previously (Whiteley, 1952) or in the same medium supplemented with 0.4 per cent sodium glutamate ("glutamate medium"). The glutamate medium supports a more rapid rate of growth, and yields cells capable of fermenting all substrates at a high rate. Since such cells have a considerably higher rate of endogenous metabolism, both media were used depending on experimental needs. Conditions of growth, harvesting, and preparation of cell suspensions have been described (Whiteley, 1952). Dried cell preparations were made by allowing a cell paste to stand for 12 to 16 hr under vacuum over several changes of P₂O₅ at room temperature. Cell free extracts were obtained by grinding with alumina according to the method of McIlwain (1948). The alumina-cell paste mixture was eluted with 0.01 M phosphate buffer at pH 6.8 and centrifuged for 20 min at 15,000 × G. Cell free extracts were also prepared by sonic disintegration in a Raytheon 10 KC oscillator. In the latter procedure, 6 to 10 g (wt wt) of cell paste were suspended in approx 25 ml of 0.01 M phosphate buffer at pH 6.8, subjected to sonic disintegration for 20 to 30 min and centrifuged for 20 min at 15,000 × G. All preparations contained a reducing agent in a final concentration of 0.001 per cent-0.05 per cent. Aged preparations are those which have been stored frozen at -4 C for 5 to 25 days. Dialysis of extracts was performed in the cold against 0.005 M cysteine (pH 7.0). The protein content of the cell free extracts was estimated by the method of Stadtman et al. (1951).

Manometric experiments were performed in an atmosphere of oxygen-free nitrogen. The Warburg vessels contained 10 to 30 mg cell protein, 50 μmoles phosphate buffer at pH 7.0, 10 to 50 μmoles of substrate, and other additions as noted. The agar modification of the Thunberg technique (Umbreit et al., 1949) was used for measurement of dehydrogenase activity.

Qualitative identification of volatile acids resulting from the fermentation of 100 to 500 μmoles of substrate in 250 ml Warburg vessels was made by partition chromatography using either silica gel columns (Elsden, 1946) or paper (Kennedy and Barker, 1951). Paper chromatography was also used for the identification of compounds containing imidazole (Ames and Mitchell, 1952), lactate (Buch et al., 1952), formamide (Wachsmann and Barker, 1955a), hydroxamic acids (Stadtman and Barker, 1950), amino acids (Levy and Chung, 1953) and α-keto acids as the 2,4-dinitrophenylhydrazones.

1 This work was supported in part by an Atomic Energy Commission Postdoctoral Fellowship at the Hopkins Marine Station and in part by a grant from the Atomic Energy Commission, Contract No. AT(45-1)-173.
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(1951). Preparations were boiled and treated with Dowex-50 before chromatography for amino acids.

Methods used for the quantitative determination of volatile acids, lactate, and ammonia and for the calculation of O/R indices have been described previously (Whiteley, 1952). Formate was determined according to Grant (1948), hydroxamic acids by the method of Lipmann and Tuttle (1945), and urocanic acid was estimated from its absorption at 277 m\(\mu\) (Mehler and Tabor, 1953).

Adenosine triphosphate (ATP) and coenzyme A (CoA) were obtained from Pabst and Co. Mesoacetic acid was obtained from Aldrich Chemical Company, Inc. I am indebted to Dr. H. Tabor for urocanic and formimino glutamic acids, to Dr. F. M. Huennekens for pyridoxal phosphate, and to Dr. H. A. Barker for citramalate.

RESULTS

Fermentable substrates. Serine, threonine, glutamate, and histidine are readily fermented by cell suspensions and dried cell preparations of M. aerogenes. Cell free extracts rapidly degrade serine and threonine but do not ferment glutamate. Histidine is fermented by some extracts but not by others.

Neither M. aerogenes nor the other species belonging to the third metabolic group of anaerobic micrococci produce gas or ammonia from the following amino acids: glycine, alanine, cysteine, cystine, valine, norvaline, methionine, leucine, norleucine, isoleucine, citrulline, arginine, phenylalanine, tyrosine, proline, hydroxyproline, tryptophan, lysine, aspartic acid, \(\alpha\)-amino butyric acid, or \(\gamma\)-amino butyric acid.

The possibility of the occurrence of a "Stickland reaction" (the oxidation of one amino acid with the concomitant reduction of another) was investigated with all available strains of Micrococcus variabilis, M. anaerobius, M. aerogenes, M. prevoti, M. activus, and M. asaccharolyticus. Two mixtures of amino acids (Stickland, 1934) were tested separately, together, and in the presence of a fermentable substrate (serine). Mixture I contained glycine, proline, and arginine; mixture II contained alanine, cysteine, and aspartic acid. When these mixtures were incubated with cell suspensions, neither gas nor ammonia was produced and dehydrogenation could not be detected. When serine was added to either mixture, the quantities of end products formed and the rate of dye decolorization indicated that only serine was degraded.

Studies with other microorganisms have shown that fermentable amino acids may be deaminated. Thus, pyruvate and \(\alpha\)-ketobutyrate arise from serine and threonine, respectively (reviewed by Snell, 1953), urocanate from histidine (reviewed by Tabor, 1954), and \(\alpha\)-keto glutarate from glutamate. Pyruvate, \(\alpha\)-ketobutyrate, and urocanate are degraded by M. aerogenes, but \(\alpha\)-keto glutarate is neither formed from glutamate nor is it fermented by any type of preparation.

Serine and threonine. The end products resulting from the fermentation of serine and threonine by dried cell preparations are given in columns 1 and 2 of table 1. Judging from the quantities of ammonia and other end products, only L-serine dehydrogenase is present in M. aerogenes. A test for residual D-serine was not performed.

During the fermentation of serine and threonine traces of pyruvic and \(\alpha\)-ketobutyric acid, respectively, have been detected. If the fermentations are carried out in an alkaline medium, or in the presence of inhibitors such as fluoride, arsenate, or arsenite (table 2), larger amounts of these keto acids are found. This suggests that the

<table>
<thead>
<tr>
<th>End Products*</th>
<th>Serine</th>
<th>Threonine</th>
<th>Glutamate</th>
<th>Histidine</th>
</tr>
</thead>
<tbody>
<tr>
<td>CO(_2)</td>
<td>9.5</td>
<td>10.0</td>
<td>9.8</td>
<td>10.3</td>
</tr>
<tr>
<td>H(_2)</td>
<td>9.6</td>
<td>9.8</td>
<td>0.5</td>
<td>0.0</td>
</tr>
<tr>
<td>Formate</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Acetate</td>
<td>9.6</td>
<td>0.0</td>
<td>10.1</td>
<td>19.1</td>
</tr>
<tr>
<td>Propionate</td>
<td>0.0</td>
<td>10.2</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Butyrate</td>
<td>0.0</td>
<td>0.0</td>
<td>4.5</td>
<td>0.5</td>
</tr>
<tr>
<td>Lactate</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>3.5</td>
</tr>
<tr>
<td>NH(_3)</td>
<td>10.2</td>
<td>10.1</td>
<td>19.9</td>
<td>29.0</td>
</tr>
<tr>
<td>% Carbon recovery</td>
<td>96</td>
<td>101</td>
<td>96</td>
<td>101</td>
</tr>
<tr>
<td>O/R index</td>
<td>1.02</td>
<td>1.0</td>
<td>0.96</td>
<td>0.96</td>
</tr>
</tbody>
</table>

* \(\mu\)Moles per 20 \(\mu\)moles DL-serine, 10 \(\mu\)moles L-threonine, 10 \(\mu\)moles L-glutamate, 10 \(\mu\)moles L-histidine. Reaction mixtures contained 25 mg protein, 50 \(\mu\)moles phosphate buffer pH 7.0, and substrate in a total volume of 2.2 ml. A dried cell preparation was used for serine and threonine fermentations and suspensions of cells grown in "peptone medium" were used for histidine and glutamate degradations.
primary conversion of the amino acids involves a deamination. No attempt has been made to determine whether one single deaminase acts on both serine and threonine, or whether two separate deaminases are required.

An initial deamination of these amino acids is further supported by the finding that the fermentation of pyruvate and α-ketobutyrate yields, except for ammonia, the same end products, and in virtually identical quantities, as that of serine and threonine, respectively. In addition, mixtures of serine and pyruvate, and of threonine and α-ketobutyrate, are decomposed at the same rates as the keto acids alone (table 3). The lower rate of gas formation from the amino acids than from the corresponding keto acids indicates that it is the initial deamination that controls the rate of decomposition. The fermentation of the keto acids is discussed in a subsequent paper (Whiteley and Ordal, 1957).

The deamination of serine and threonine appears to be mediated by dehydrase(s), with pyridoxal phosphate as the coenzyme, in some bacteria (reviewed by Snell, 1953), whereas adenylic acid and glutathione (Wood and Gunsalus, 1949), and biotin and adenylic acid (Lichstein and Umbreit, 1947) have been reported as stimulatory in deamination by other bacteria. Preparations of *M. aerogenes* aged according to the method of Lichstein and Christman (1948) failed to show any stimulation in the deamination of serine when biotin, adenylic acid, or biotin plus adenylic acid were added. Attempts to dissociate cofactors participating in the deamination of serine by dialysis of extracts were unsuccessful. However, a few extracts which had been aged by prolonged storage in the cold, showed a 50 per cent increase in serine deamination when pyridoxal phosphate was added. Glutathione and adenylic acid had no effect.

**Glutamate.** Cell suspensions and dried cell preparations degrade glutamate readily to form the end products shown in column 3 of table 1 but cell free extracts capable of degrading glutamate could not be prepared. Glutamine (not shown) is fermented by cell suspensions and dried cell preparations at the same rate as glutamate and yields the same end products except that twice the amount of ammonia is formed. It will be noted that approx 1 μmole of carbon dioxide and acetate are formed per μmole of glutamate decomposed. This observation, coupled with the finding that none of the acids of the tricarboxylic acid cycle are fermented, indicates that glutamate degradation does not occur via the tricarboxylic acid cycle. The amount of hydrogen produced may vary but generally does not exceed 1.0 μmoles of glutamate, and lactate is not formed. No free organic acids other than acetate and butyrate have been found either as end products or as intermediates in fermentations with or without inhibitors. The CoA and phosphate derivatives of acetate and butyrate were the only activated compounds that could be detected in reaction mixtures in the course of fermentation.

Mesaconate, citramalate and pyruvate have

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**TABLE 2**

<table>
<thead>
<tr>
<th>Compound</th>
<th>Final Concentration</th>
<th>Serine*</th>
<th>Threonine*</th>
<th>Glutamate</th>
<th>Histidine*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fluoride</td>
<td>0.04</td>
<td>53†</td>
<td>55</td>
<td>15</td>
<td>70</td>
</tr>
<tr>
<td>Cyanide</td>
<td>0.008</td>
<td>129</td>
<td>150</td>
<td>24</td>
<td>133</td>
</tr>
<tr>
<td>Arsenite</td>
<td>0.008</td>
<td>81</td>
<td>85</td>
<td>104</td>
<td>93</td>
</tr>
<tr>
<td>Arsenate</td>
<td>0.008</td>
<td>36</td>
<td>45</td>
<td>7</td>
<td>40</td>
</tr>
</tbody>
</table>

* Essentially identical values were obtained from serine and pyruvate, threonine and α-ketobutyrate, and histidine and urocanate.
† Total gas as per cent of control without inhibitor. Reaction mixture: 20 μmoles substrate, 25 mg protein, 50 μmoles phosphate buffer (pH 6.5 for α-keto acids and pH 7.0 for others) in 2.2 ml. Inhibitors mixed with reaction mixture 30 min before addition of substrate.

**TABLE 3**

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Total Gas/10 Min</th>
<th>μL</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Serine</td>
<td></td>
<td>179</td>
</tr>
<tr>
<td>2. Pyruvate</td>
<td></td>
<td>225</td>
</tr>
<tr>
<td>3. Serine and pyruvate</td>
<td></td>
<td>224</td>
</tr>
<tr>
<td>4. Threonine</td>
<td></td>
<td>130</td>
</tr>
<tr>
<td>5. α-Ketobutyrate</td>
<td></td>
<td>162</td>
</tr>
<tr>
<td>6. Threonine and α-Ketobutyrate</td>
<td></td>
<td>169</td>
</tr>
</tbody>
</table>

Same reaction mixture as for table 1 with 40 μmoles of pyruvate and α-ketobutyrate and 80 μmoles of DL-serine and DL-threonine.
been shown to be intermediates in the fermentation of glutamate by Clostridium tetanomorphum (Wachsman and Barker, 1955b; Barker et al., 1956; Wachsman, 1956). Mesaconate and citramalate are not fermented by any preparation of M. aerogenes and can be quantitatively recovered from reaction mixtures. As stated above, pyruvate is readily degraded by M. aerogenes but differences have been found in the end products formed from pyruvate and glutamate. Suspensions of cells of M. aerogenes grown in peptone medium form carbon dioxide, hydrogen, acetate, lactate, and traces of butyrate from pyruvate (Whiteley and Ordal, 1957), whereas carbon dioxide, hydrogen, acetate and butyrate are formed from glutamate (table 1). A comparison of the rates of fermentation of a mixture of pyruvate and glutamate (table 4) with the rate of degradation of each compound separately has shown that the mixture is fermented at a rate exceeding the sum of the individual rates. Differences have also been found in the effects of metabolic inhibitors on pyruvate and glutamate fermentations (table 2).

The fermentation of glutamate is not dependent on the type of preparation used and is not influenced by the addition of ATP or CoA, or by acetate, γ-aminobutyrate, acetacacetate, β-OH butyrate, crotonate, formate, or formamido. The last 2 compounds could be considered as possible end products in histidine fermentation and were added to determine whether the glutamate fermentation could be altered to resemble that of histidine. The other compounds added may be possible participants or intermediates in butyrate formation and were added to fermentations of glutamate in both nitrogen and hydrogen atmospheres to determine whether the amount of butyrate could be increased. Similar experiments were carried out in which these compounds were added to fermentations of pyruvate. Neither the rate of fermentation nor the quantities of end products formed were altered by the addition of these compounds although the preparations are capable of dehydrogenating β-OH butyrate at a low rate and are able to activate acetacacetate and β-OH butyrate.

Histidine. Investigations of the pathway of histidine degradation in tissues and bacteria have shown that the first step is deamination to urocanate (Tabor, 1954). Since this compound can be degraded by M. aerogenes at a rate comparable to that of histidine (table 5), it appeared likely that urocanate was an intermediate in histidine fermentation by M. aerogenes. The following experimental results have been obtained which support this possibility: (1) urocanate is formed, as determined by spectrophotometry and paper chromatography, during the fermentation of histidine, and larger amounts of urocanate can be made to accumulate by the addition of fluoride, arsenate, and arsenite, or by carrying out the fermentation in an alkaline medium; (2) except for ammonia, the same end products are formed in essentially identical quantities from the fermentation of histidine and urocanate; (3) a mixture of urocanate and histidine is fermented at the same rate as either compound separately (table 5); and (4) the fermentation of both compounds is affected in the same way by the addition of various inhibitors (table 2).

It has been shown (Tabor, 1954) that in tissues and other microorganisms urocanate is further degraded via formamido-L-glutamic acid and formyl-L-glutamic acid to glutamate, ammonia and formate, or in C. tetanomorphum (Wachsman

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### TABLE 4

Rates of fermentation of glutamate and pyruvate by dried cell preparation of Micrococcus aerogenes

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Total Gas/20 Min</th>
<th>μL</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Pyruvate</td>
<td></td>
<td>47</td>
</tr>
<tr>
<td>2. Glutamate</td>
<td></td>
<td>50</td>
</tr>
<tr>
<td>3. Pyruvate and glutamate</td>
<td></td>
<td>130</td>
</tr>
</tbody>
</table>

Reaction mixture as for table 1 with 40 μmoles of each substrate, and 50 mg protein.

### TABLE 5

Rates of fermentation of histidine, urocanate, and glutamate by dried cell preparations of Micrococcus aerogenes

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Total Gas/10 Min</th>
<th>NH₃/10 Min</th>
<th>μL</th>
<th>μmoles</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Histidine</td>
<td></td>
<td></td>
<td>101</td>
<td>6.2</td>
</tr>
<tr>
<td>2. Urocanate</td>
<td></td>
<td></td>
<td>93</td>
<td></td>
</tr>
<tr>
<td>3. Histidine and urocanate</td>
<td></td>
<td></td>
<td>106</td>
<td></td>
</tr>
<tr>
<td>4. Glutamate</td>
<td></td>
<td></td>
<td>105</td>
<td>4.4</td>
</tr>
<tr>
<td>5. Histidine and glutamate</td>
<td></td>
<td></td>
<td>169</td>
<td>9.1</td>
</tr>
</tbody>
</table>

Reaction mixture as for table 1 with 40 μmoles of each substrate. Ammonia not determined in 2) and 3) above.
and Barker, 1955a) and Aerobacter aerogenes (Magasanik, 1953) to glutamate and formamide. Neither glutamate nor formyl derivatives of glutamate could be detected during the fermentation of histidine by M. aerogenes. However, if M. aerogenes degrades histidine by either of the 2 pathways described above, glutamate would not accumulate since it is a fermentable substrate. It would be anticipated then that the quantities of end products formed from histidine would be identical with those formed from glutamate except for the additional ammonia and formate (or formamide) and that compounds which inhibit glutamate fermentation would also inhibit histidine fermentation. However, considerable differences are found in the effect of various inhibitors (table 2) and in the end products formed from glutamate and histidine (columns 3 and 4 of table 1). Lactate is produced from histidine but not from glutamate, and the amounts of acetate and butyrate formed are quite dissimilar. Formamide was not found and only traces of formate are produced from histidine. As stated above, the addition of formate or formamide does not influence the fermentation of glutamate, nor does it affect the degradation of histidine. Neither formamide nor formate is degraded by M. aerogenes when tested alone or with a fermentable substrate.

**DISCUSSION**

It appears likely that all preparations of M. aerogenes degrade serine and threonine via pyruvate and α-ketobutyrate, respectively, as intermediates. This conclusion is supported by the finding that these α-keto acids may be isolated from fermentations of the amino acids. Further support comes from a comparison of the degradation of serine and threonine with their respective α-keto acids with regard to the quantities of end products, rates of fermentation and effects of inhibitors. The formation of pyruvate from serine by aged preparations of M. aerogenes requires pyridoxal phosphate but not glutathione or adenlyc acid. Hence the enzyme mediating this reaction in M. aerogenes resembles the L-serine dehydrase of Neurospora (Yanofsky and Reissig, 1953) rather than the serine deaminase of Escherichia coli (Wood and Gunsalus, 1949).

The fermentation of glutamate by M. aerogenes yields the same products as that by C. tetanomorphum (Barker, 1937), so that it seemed possible that the same mechanism of degradation could be involved. For C. tetanomorphum this has been shown (Wachsman and Barker, 1955b; Barker et al., 1956; Wachsman, 1956) to implicate mesaconate, citramalate, pyruvate, and α-keto-glutarate. M. aerogenes is not able to degrade mesaconate, citramalate, or α-keto-glutarate and these compounds could not be detected in reaction mixtures fermenting glutamate. It is possible, however, that activated derivatives of mesaconate and citramalate are involved but are formed transiently and in such small amounts that they have not been detected in reaction mixtures. Further, pyruvate is the source of butyrate in the fermentation of glutamate by C. tetanomorphum (Wachsman and Barker, 1955b), whereas M. aerogenes produces only traces of butyrate from pyruvate, although substantial amounts of this acid are formed from glutamate. The effects of adding various inhibitors to fermentations of pyruvate and glutamate and the increased rate of fermentation of mixtures of these two compounds also suggests that pyruvate may not be a normal intermediate in the decomposition of glutamate.

Butyrate formation in M. aerogenes could occur by the pathway found in other bacteria (reviewed by Barker, 1951) since extracts are able to activate acetate, acetoacetate, β-OH butyrate and also are able to dehydrogenate β-OH butyrate. However, the quantity of butyrate formed either from pyruvate or from glutamate was not increased by the addition of acetate, acetoacetate, β-OH butyrate, or crotonate, together with ATP and CoA, under any conditions of testing. The amount of butyrate formed from glutamate was not altered by the addition of pyruvate.

Experimental results of studies on the degradation of histidine by M. aerogenes indicate that the first step is a deamination to urocanate. It does not seem possible that urocanate could be then degraded via urea, acrylate, or imidazole, since none of these compounds is decomposed by M. aerogenes, nor is imidazole carboxylic acid. It appears unlikely, also, that urocanate is degraded via glutamate or that histidine fermentation could be considered the equivalent of glutamate fermentation with formate and ammonia as additional end products. This statement is supported by the following experimental findings: (1) different amounts of acetate, butyrate and lactate are formed from histidine and glutamate, (2) the fermentations of histidine and glutamate are affected differently by inhibitors, (3) rate
determinations show independent degradations of the two substrates, and (4) extracts of M. aerogenes have been prepared which are able to ferment histidine but not glutamate.

It is possible, however, that a derivative of glutamate is formed from histidine and is degraded differently than glutamate supplied exogenously. Activated amino acids have been reported (Hoagland et al., 1956; Cantoni, 1952) and it is conceivable that activated glutamate, existing as such or bound to an enzyme, could be produced from histidine. It is also possible that the presence of formate (or the equivalent) and ammonia produced from histidine, alters the fermentation of glutamate formed as an intermediate. A condensation of formate (or its equivalent), with a C₂ compound produced from glutamate could result in the formation of pyruvate, thereby providing a hydrogen acceptor and diverting “available hydrogen” from butyrate formation. Preliminary experiments with labeled formate indicate that the above condensation reaction can occur in M. aerogenes and similar results have been obtained with other anaerobic micrococci (Novelli, 1955). Failure to change the fermentation of glutamate with respect to end products by the addition of formate and suitable cofactors may be attributed to the fact that the degradation of histidine does not result in the release of free formate from the intermediate compounds (Tabor and Rabinowitz, 1956).

ACKNOWLEDGMENTS

It is a pleasure to thank Drs. H. C. Douglas, C. B. van Niel, and E. J. Ordal for suggestions and many helpful discussions in the course of this work. I wish to thank Mr. John Murphy for technical assistance in part of this work.

SUMMARY

Quantitative data for the fermentation of serine, threonine, glutamate and histidine by strain 228 of Micrococcus aerogenes are presented. A “Stickland reaction” does not occur in this strain or in any of the related anaerobic micrococci.

Serine is degraded to ammonia, carbon dioxide, hydrogen, and acetate with pyruvate as an intermediate product. The deamination of serine is stimulated by pyridoxal phosphate but not by biotin, glutathione, adenylic acid or combinations of these cofactors.

Threonine is fermented to ammonia, carbon dioxide, hydrogen, and propionate, with α-keto- butyrate as an intermediate.

Glutamate is degraded to ammonia, carbon dioxide, hydrogen, acetate and butyrate. Meso- conate, citramalate and α-ketoglutarate are not formed from glutamate or degraded by any preparation of M. aerogenes.

Histidine is fermented to ammonia, carbon dioxide, acetate, butyrate, lactate, and traces of formate, with urocanate as an intermediate product. A comparison of end products, as well as other experimental evidence, indicates that if glutamate is formed as an intermediate product in histidine fermentation, its subsequent degradation is different from that of exogenously supplied glutamate.

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