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Thauer R K, Jungermann K & Decker K. Energy conservation in chemotrophic anaerobic bacteria. *Bacteriol. Rev.* 41:100-80, 1977.
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This is a treatise on the thermodynamic and mechanistic principles of energy conservation in bacteria that live in biotopes without light and molecular oxygen. Evidence is summarized that these microorganisms are capable of electron transport phosphorylation, a mechanism previously thought to be restricted to phototrophs and aerobes. [The *SCI*® indicates that this paper has been cited in over 575 publications.]

Energetics of Anaerobes

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From 1965 to 1972, as graduate students and then postdoctoral fellows in Karl Decker's laboratory at Freiburg University, Kurt Jungermann and I studied the energy metabolism of *Clostridium kluyveri*. This is a rather unique anaerobe that grows at the expense of ethanol plus acetate symproportionation to butyrate and caproate.

It had been proposed that this fermentation is coupled with adenosine 5'-triphosphate (ATP) synthesis by electron transport phosphorylation, a mechanism that at the time was thought to be restricted to aerobes and phototrophs. We found that the proposal was based on incomplete data on the fermentation products formed and that ATP is generated by substrate-level phosphorylation. Despite this "negative" result we remained interested in the organism since there was still an intriguing thermodynamic problem to be solved: *C. kluyveri* obtains energy for growth from a fermentation whose associated free-energy change is small relative to that required for the synthesis of 1 mol ATP. The mechanism of energy conservation, therefore, must be such as to allow fractional stoichiometries of ATP formation. How this is achieved was not known.

In 1970 we published a first general treatise on the subject.[1] It was an attempt to analyze the energy metabolism of anaerobic bacteria applying mechanistic and thermodynamic rules for the prediction of metabolic pathways, ATP gains, and growth yields. This approach proved very fruitful and was adopted by many microbiologists. In 1976 Ralph Wolfe (Urbana, Illinois) encouraged us to write an updated version for *Bacteriological Reviews*.

This paper became a *Citation Classic* probably because it contains a lot of information not otherwise available and probably also because it points out many problems that were taken up by investigators. We obtained more than 1,000 reprint requests. I myself, during writing, became interested in the energy metabolism of methanogenic bacteria, sulfate-reducing bacteria, and sulfur-reducing bacteria. For these anaerobes we predicted that energy is conserved via electron transport phosphorylation, which, in later studies, turned out to be correct.[2-5]

1. **Decker K, Jungermann K & Thauer R K.** Wege der Energiegewinnung in Anaerobiern. *Angew. Chem.* 82:153-73, 1970. (Cited 30 times.) (Also published as Energy production in anaerobic organisms. *Angew. Chem. Int. Ed.* 9:138-58, 1970. [Cited 70 times.])
2. **Thauer R K & Morris J G.** Metabolism of chemotrophic anaerobes. Old views and new aspects. (Kelly D P & Carr N G, eds.) *The microbe 1984. Part II. Prokaryotes and eukaryotes.* Cambridge, England: Cambridge University Press, 1984. p. 123-68. (Cited 5 times.)
3. **Thauer R K.** Nickelenzyme im Stoffwechsel von methanogenen Bakterien (Nickel enzymes in methanogenic bacteria). *Biol. Chem. Hoppe-Seyler* 366:103-12, 1985.
4. ————. Citric acid cycle, 50 years on: modifications and an alternative pathway in anaerobic bacteria. *Eur. J. Biochem.* 176:497-508, 1988.
5. **Thauer R K, Möller-Zinkhan D & Spormann A.** Biochemistry of acetate catabolism in anaerobic chemotrophic bacteria. *Annu. Rev. Microbiol.* (In press.)

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