Biochemistry and Physiology of Anaerobic Bacteria

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To the memory of Harry D. Peck, Jr. (1927–1998) professor, founder, and chairman of the Department of Biochemistry at the University of Georgia and pioneer in studies of sulfate-reducing bacteria and hydrogenases.

Preface

During the last thirty years, there have been tremendous advances within all realms of microbiology. The most obvious are those resulting from studies using genetic and molecular biological methods. The sequencing of whole genomes of a number of microorganisms having different physiologic properties has demonstrated their enormous diversity and the fact that many species have metabolic abilities previously not recognized. Sequences have also confirmed the division of prokaryotes into the domains of Archaea and bacteria. Terms such as hyper- or extreme thermopiles, thermophilic alkaliphiles, acidophiles, and anaerobic fungi are now used throughout the microbial community. With these discoveries has come a new realization about the physiological and metabolic properties of microoganisms. This, in turn, has demonstrated their importance for the development, maintenance, and sustenance of all life on Earth. Recent estimates indicate that the amount of prokaryotic biomass on Earth equals—and perhaps exceeds—that of plant biomass. The rate of uptake of carbon by prokaryotic microorganisms has also been calculated to be similar to that of uptake of carbon by plants. It is clear that microorganisms play extremely important and typically dominant roles in recycling and sequestering of carbon and many other elements, including metals.

Many of the advances within microbiology involve anaerobes. They have metabolic pathways only recently elucidated that enable them to use carbon dioxide or carbon monoxide as the sole carbon source. Thus they are able to grow autotrophically. These pathways differ from that of the classical Calvin Cycle discovered in plants in the mid-1900s in that they lead to the formation of acetyl-CoA, rather than phosphoglycerate. The new pathways are prominent in several types of anaerobes, including methanogens, acetogens, and sulfur reducers. It has been postulated that approximately twenty percent of the annual circulation of carbon on the Earth is by anaerobic processes. That anaerobes carry out autotrophic type carbon dioxide fixation prompted studies of the mechanisms by which they conserve energy and generate ATP. It is now clear that the pathways of autotrophic carbon dioxide fixation involve hydrogen metabolism and that they are coupled to electron transport and generation of ATP by chemiosmosis. Enzymes catalyzing the metabolism of carbon dioxide, hydrogen, and other materials for building cell material and for electron transport are now intensely studied in anaerobes. Almost without exception, these enzymes depend on metals such as iron, nickel, cobalt, molybdenum, tungsten, and selenium. This pertains also to electron carrying proteins like cytochromes, several types of iron-sulfur and flavoproteins. Much present knowledge of electron transport and phosphorylation in anaerobic microoganisms has been obtained from studies of sulfate reducers. More recent investigations with methanogens and acetogens corroborate the findings obtained with the sulfate reducers, but they also demonstrate the diversity of mechanisms and pathways involved.

This book stresses the importance of anaerobic microorganisms in nature and relates their wonderful and interesting metabolic properties to the fascinating enzymes that are involved. The first two chapters by H. Gest and H.G. Schlegel, respectively, review the recycling of elements and the diversity of energy resources by anaerobes. As mentioned above, hydrogen metabolism plays essential roles in many anaerobes, and there are several types of hydrogenase, the enzyme responsible for catalyzing the oxidation and production of this gas. Some contain nickel at their catalytic sites, in addition to iron-sulfur clusters, while others contain only iron-sulfur clusters. They also vary in the types of compounds that they use as electron carriers. The mechanism of activation of hydrogen by enzymes is discussed by Simon P.J. Albracht, and the activation of a purified hydrogenase from *Desulfovibrio vulgaris* and its catalytic center by B. Hanh Huynh, P. Tavares, A.S. Pereira, I. Moura, and J.G. Moura. The biosynthesis of iron-sulfur clusters, which are so prominent in most hydrogenases, formate and carbon monoxide dehydrogenases, nitrogenases, many other reductases, and several types of electron carrying proteins, is explored by J.N. Agar, D.R. Dean, and M.K. Johnson. R.J. Maier, J. Olson, and N. Mehta write about genes and proteins involved in the expression of nickel dependent hydrogenases. Genes and the genetic manipulations of *Desulfovibrio* are examined by J.D. Wall and her research associates. In Chapter 8, G. Voordouw discusses the function and assembly of electron transport complexes in *Desulfovibrio vulgaris*. In the next chapter Richard Cammack and his colleagues introduce eukaryotic anaerobes, including anaerobic fungi and their energy metabolism. They explore the role of the hydrogenosome, which in the eukaryotic anaerobes replaces the mitochondrion. A rather new aspect related to anerobic microorganisms is the observation that they exhibit some degree of tolerance toward oxygen. They typically lack the known oxygen stress enzymes superoxide dismutase and catalase, but they contain novel iron-containing protein including hemerythrin-like proteins, desulfoferrodoxin, rubrerythrin, new types of rubredoxins, and a new enzyme termed superoxide reductase. D.M. Kurtz, Jr., discuses in Chapter 10 these proteins and proposes that they function in the defense toward oxygen stress in anaerobes and microaerophiles. Over six million tons of methane is produced biologically each year, most of it from acetate, by methanogenic anaerobes. J.G. Ferry describes in Chapter 11 that reactions include the activation of acetate to acetyl-CoA, which is cleaved by acetyl-CoA synthase. The methyl group is subsequently reduced to methane, and the carbonyl group is oxidized to carbon dioxide. The pathway is similar but reverse of that of acetyl-CoA synthesis by acetogens, but it involves cofactors unique to the methane-producing Archaea. Selenium has been found in several enzymes from anaerobes including species of clostridia, acetogens, and methanogens. In Chapter 12, W.T. Self has summarized properties of selenoenzymes, that are divided into three groups. The first constitutes amino acid reductases that utilize glycine, sarcosine, betaine, and proline. In these and also in the second group, which includes formate dehydrogenases, selenium is present as selenocysteine. Selenocysteine is incorporated into the polypeptide chain via a special seryl-tRNA and selenophosphate. The third group of selenoenzymes is selenium-molybdenum hydroxylases found in purinolytic clostridia. The nature of the selenium in this group has yet to be determined. Chapters 13 and 14 deal with acetogens, which produce anaerobically a trillion kilograms of acetate each year by carbon dioxide fixation via the acetyl-CoA pathway. H.L. Drake and K. Küsel highlight the diversity of acetogens and their ecological roles. A. Das and L.G. Ljungdahl discuss evidence that the acetyl-CoA pathway of carbon dioxide fixation is coupled with electron transport and ATP generation. In addition, they present some data showing how acetogens can deal with oxydative stress. In Chapter 15, D.P. Kelly discusses the biochemical features common to both anaerobic sulfate reducing bacteria and aerobic thiosulfate oxidizing thiobacilli. His chapter is also a tribute to Harry Peck. The last three chapters are devoted to the reduction by anaerobic bacteria of metals, metalloids and nonessential elements. L.L. Barton, R.M. Plunkett, and B.M. Thomson in their review point out the geochemical importance these reductions, which involve both metal cations and metal anions. J. Wiegel, J. Hanel, and K. Aygen describe the isolation of recently discovered chemolithoautotrophic thermophilic iron(III)-reducers from geothermally heated sediments and water samples of hot springs. They propose that these bacteria are ancient and were involved in formation of iron deposits during the Precambrian era. The last chapter is a discussion of electron flow in ferrous bioconversion by E.J. Laishley and R.D. Bryant. They visualize a model for biocorrosion by sulfate-reducing bacteria that involves both iron and nickel-iron hydrogenases, high molecular cytochrome, and electron transport using sulfate as an acceptor.

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