

Preface

Methanogens are prokaryotic microorganisms that produce methane as an end-product of their metabolism. They are strictly anaerobic archaea belonging to the taxon Euryarchaeota. Methanogens occupy a wide variety of anaerobic environments, even extreme habitats characterized by high temperature, salinity, and extreme pH (Liu and Whitman 2008). More temperate habitats include marine and freshwater sediments, flooded soils, landfills, anaerobic digesters, geothermal systems, and the heartwood of trees. Notably, methanogens also thrive in the cytoplasm of anaerobic unicellular eukaryotes and in the gastrointestinal tracts of animals and humans. Frequently, they attach to the internal surfaces of the gastrointestinal tracts and of the protists living in intestinal environments with the aid of special adhesion-like proteins (Liu and Whitman 2008). In insect guts, methanogens have to cope with a very special environment, since they are exposed to a continuous influx of oxygen through the gut wall that challenges the strictly anaerobic symbionts. Notwithstanding that methanogens are very diverse, they can use only a very restricted number of substrates. They are unable to use organic substances (with the exception of acetate and formate), and consequently, methanogens must rely on CO_2 and methyl-group containing compounds and acetate, which are provided by the fermentations performed by complex anaerobic bacterial communities. The methanogenic substrates are predominantly metabolized with the aid of H_2 that is provided by syntrophic bacterial communities or, in the case of certain anaerobic protists, by the action of specialized mitochondrion-derived organelles, the hydrogenosomes. Since both hydrogenosomes and syntrophic bacterial communities rely on a low concentration of H_2 , the interspecies hydrogen transfer that is mediated by methanogens is crucial for the proper functioning of hydrogenosomes and syntrophic anaerobic bacterial communities.

The synthesis of methane follows a complex biochemical pathway that is characterized by a number of unique coenzymes and membrane-bound enzyme complexes. It has been reviewed recently by Hedderich and Whitman (2006). CO_2 is reduced to methane by H_2 in hydrogenotrophic methanogens, which represent the majority of the methanogens living in symbiosis with protists and multicellular animals. The second type of substrate, methylgroup containing compounds

including methanol, methylated amines, and methylated sulfides, is used by methylotrophic methanogens, which are predominantly found in the gastrointestinal tracts of mammals and insects. The third type of substrate is acetate, which is metabolized by acetoclastic methanogens. Although only two genera (*Methanosarcina* and *Methanosaeta*) use acetate as substrate, as much as two-thirds of the biologically generated methane is derived from acetate. Notably, acetoclastic methanogens are rare among the symbiotic methanogens. This is not surprising since symbiotic acetoclastic methanogens compete with their hosts for acetate. Notwithstanding, an acetoclastic methanogen has recently been identified as endosymbiont in the free-living protist *Metopus es* (Narayanan et al. 2009).

Methanogens are abundant in habitats where electron acceptors such as O_2 , NO_3^- , Fe^{3+} , and SO_4^{2-} are limiting (Liu and Whitman 2008). In such methanogenic habitats, complex organic matter is degraded to methane by the syntrophic action of different groups of anaerobic bacteria. Organic polymers are degraded initially by specialized bacteria to sugars, lactate, short-chain fatty acids, and alcohols. These products are further fermented by other bacteria to acetate, formate, H_2 , and CO_2 , which are the substrates used by methanogens. These methanogens catalyze the terminal step in the anaerobic food chain by converting the various methanogenic substrates to methane, which is released into the atmosphere. More than 70% of the annual global methane emission (ranging from 500 to 600 Tg CH_4 /year) stem from biological methanogenesis and contribute significantly to global warming. (Whitman et al. 2006). The symbiotic methanogens in the gastrointestinal tract of ruminants and other “methanogenic” mammals contribute significantly to the global methane budget. Especially the rumen hosts an impressive diversity of methanogens, which have been studied using culture-independent 16S rRNA methods (Janssen and Kirs 2008; Wright et al. 2004). Insects, particularly termites, also host very complex methanogenic communities, but they release much less methane due to the concomitant oxidation of methane in the soil and the termite mounds. On the other hand, the contributions by the methanogenic endosymbionts of protists living in freshwater sediments can be neglected (van Hoek et al. 2006).

This monograph deals with methanogenic endosymbionts of free-living and symbiotic protists, episymbionts of rumen ciliates, methanogenic endosymbionts of ciliates, and termite flagellates, which are accompanied by bacterial endosymbionts, and methanogens in the gastrointestinal tract of vertebrates and arthropods. One review summarizes our knowledge about the genomic consequences of living together in symbiotic associations; another review discusses the role of methanogens in syntrophic degradation. Finally, the current state of information about hydrogenosomes has been reviewed.

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