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Rumen Methanogens Community as Drivers of Methane Emission

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Abstract

Among the vast and diverse ruminal micro-biota, Archaea account up to 3-4% of the entire microbial population in rumen of ruminants. *Methanobrevibacter gottschalkii, Methanobrevibacter thaueri, Methanobrevibacter smithii and Methanosphaera stadtmanae* are common ruminal methanogens. Majority of archea are hydrogenotrophic over acetoclastic methanogen in rumen. Methanogens are endowed with co-enzymes that enable them to produce biogenic methane than other microbes. Biogenic methane produced from ruminants has a significant contribution to global warming. So this review enlightened the complete pictures of methanogens in ruminants and their relationships with other ruminal microbes. The study concluded that the methanogen composition remained variable among ruminant species and these dynamics emanated from animal factors, management and geographical variations.

Keywords: Composition; Diversity; Methanogens; Ruminants; Substrate

Introduction

The inherent characteristics of rumen makes it unique anaerobic habitat to accommodate a community of archaea. Archaea account up to 3-4% of the entire microbial population in the rumen of ruminants (Sharp *et al.* 1998; Yanagita *et al.* 2000 and Ziemer *et al.* 2000) [1-3]. The diversity and population of archaea is very low when compared with bacteria (Lin *et al.* 1997 and Mackie *et al.* 2000) [4,5]. Nearly all of these domain are methanogens, most of which are hydrogenotrophic rather than acetoclastic.

Most of methanogens live freely in rumen liquid or as members of the biofilm adhering to feed particles (Wang *et al.* 2011; Belanche *et al.* 2014 and Jiao *et al.* 2015) [6-8], whereas a small portion of ruminal methanogens are symbionts with protozoa, either ectosymbionts or endosymbionts (Ohene-Adjei *et al.* 2007; Tymensen and McAllister 2012 and Valle *et al.* 2015) [9-11]. There are several possible substrates for methanogenesis in the rumen that originate from bacterial, fungal and protozoa fermentation, including hydrogen (H_2), carbon-dioxide (CO_2), formate, acetate and methyl compounds (Hook *et al.* 2010) [12]. Among which, H_2 and CO_2 are predominant substrates for methanogenesis in the rumen (Hungate *et al.* 1970; Hobson *et al.* 1997; Cavicchioli 2011) [13-15]. There is a strong connection between microbial fermentation processes for H_2 and CH_4 formation by methanogenic archaea in the rumen (Janssen 2010) [16]. Accordingly, methanogens interact with other ruminal microbes, including protozoa (Vogels *et al.* 1980) [17], bacteria (Hegarty and Klieve 1999) [18] and fungi (Brul and Stumm 1994) [19] through interspecies H_2 transfer. Therefore, this review is aimed at understanding of ruminal methanogen community structure, forms, main substrate used and methanogen pathways and hypothesizing a scope for future studies.

Structure and biochemistry of methanogens

Methanogens are a domain of Archaea which has been defined as a separate domain from bacteria and eukaryotes based on the specific 16S ribosomal sequences (Woese *et al.* 1978 and Schafer *et al.* 1999) [20,21]. Methanogens differ from bacteria by the presence of membrane lipids consisting of diether or tetraether linked isoprenoids (De Rosa and Gambacorta 1988) [22] and lack of muramic acid containing peptidoglycans, though some species may have a pseudomuramic acid (Kandler and Hippe 1977) [23]. Another variation between methanogens and bacteria is the structure of archaeal ribosomes. The subunit structure of archaeal ribosomes has a closer resemblance to eukaryotes than true bacteria and the transcription machinery, and the structure of DNA dependent RNA polymerase is also different (Schafer *et al.* 1999) [21].

Forms of methanogens

Free living methanogens

Most of methanogens are free living which is not associated with rumi¬nal protozoa or fungi (Belanche *et al.* 2014) [7]. Majority of free-living methanogens are integrated into biofilm on the surface of feed particles where H_2-producing bacteria actively produce H_2 (Leng 2014) [24]. These methanogens may not be inhibited as much as free-living peers by anti-methanogenic inhibitors. None of the Sequences related to *Methanobacterium* and *Methanosphaera* have been recovered from rumen protozoa and, thought to be free-living methanogens. In contrast, a significant portion (32.8%) of the *Methanobrevibacter* sequences archived in Ribosomal Database Project (RDP) was recovered from protozoa. However, *Methanobrevibacter* accounts for at least 65% of the rumen methanogens in which significant portion of the *Methanobrevibacter* sequences are not free living may simply reflect the probability of sequence recovery, rather than a selective association between rumen protozoa and *Methanobrevibacter.* It is reflected by smaller number of 16S rRNA gene sequences recovered from protozoa than from rumen content or fluid. The result could also arise from difficulties associated with obtaining archaeal DNA from protozoal cells (Belanche *et al.* 2014) [7].

Protozoa associated methanogens (PAM)

Most species of rumen ciliate protozoa contain hydrogenosomes, a unique type of membrane bounded organelles producing H_2 by malate oxidization (Muller 1993) [25]. These organelles can attract some methanogens as endosymbionts (Janssen and Kirs 2008) [26]. Hydrogen generated by rumen protozoa could be utilized by PAM, which benefits both parties. Methanogens have been found internally (Finlay *et al* 1994) [27] and externally in association with protozoa (Vogels *et al.* 1980 and Krumholz *et al.* 1983) [17,28]. Stumm *et al.* (1982) [29], observed that the frequency of ectosymbiotic methanogens was affected by relative contribution of H_2 production by rumen ciliates and H_2-producing bacteria. Based on fluorescence in situ hybridization analysis, about 16% of the rumen ciliates contained methanogens inside their cells (Lloyd *et al.* 1996) [30]. A possible explanation for low incidence is that intracellular association may be transient rather than permanent. However, earlier studies indicated that rumen ciliates do not have endosymbiotic methanogens though they might have ectosymbiotic methanogens (Williams and Coleman, 1992) [31]. The difficulty in distinguishing engulfed methanogens from true endosymbiotic methanogens presents a challenge in determining if rumen ciliates possess true endosymbiotic methanogens and or bacteria. Because of labor intensive procedures, PAM are mostly identified using DNA based methods, and only one strain of methanogens (isolates MB-9, related to Methanobrevibacter ruminantium) has been reported to be associated with a ciliate in the rumen of sheep (Tokura 1999) [32]. Among the methanogen sequences of rumen origin archived in the RDP database (Release 11, Update 3), only a very small proportion (5.3%) was recovered from washed protozoa cell (Chagan et al. 1999; Tokura *et al.* 1999; Regensbogenova et al. 2004; Ohene-Adjei *et al.* 2004; Tymensen and McAllister 2012) [10,32-35]. *Methanobrevibacter* and *Methanomicrobium* were the first and second largest genera reported to be PAM, and they accounted for 32.8% and 23.0% of the total sequences, respectively. Methanomicrobium is better represented in PAM sequences than total archaeal sequences (7.7%), species of both taxa may be among the predominant PAM. However, Janssen and Kirs (2008) [26], declared that the above results may be biased because only a small number of PAM sequences were obtained from selected protozoa. Besides, the PAM sequences may be contaminated with sequences of non-PAM.

Rumen methanogens population

Most of the ruminant methanogens are known to be resident of rumen and belong to three principal genera including *Methanobrevibacter, Methanomicrobium* and 'rumen cluster C' (Paul *et al.* 2012) [36], while the rest belong to minority genera such as *Methanimicrococcus, Methanosarcina* and *Methanobacterium* (Janssen and Kirs 2008; St-Pierre and Wright 2013) [26,37]. A varieties of methanogens can be found in the rumen (Janssen and Kirs 2008; Gemma *et al.* 2015) [26,38]. Gemma *et al.* (2015) noted that 77.7% of methanogens in the rumen were hydrogenotrophic, while 22.1% had an ability to grow with H_2 and methyl groups derived from methanol or methylamines. According to earlier study by Kim *et al.* (2011) [39], the Archaea in rumen of domesticated livestock deposited in the Ribosomal Database Project (RDP) accounts 3516 archaeal sequences. During that time, the species of archaea in the rumen is estimated to be approximately 949 and with estimated maximum number of species 1469 (Kim *et al.* 2011) [39]. Nearly all the archaeal sequences were assigned to the phylum Euryarchaeota which was represented by about 670 genus-level OTUs and 1000 species-level OTUs. Compared with other anaerobic habitats, greater than

100 species of methanogens of 28 genera have been isolated, the diversity and species richness of ruminal methanogens are quite low, reflecting the highly selective ruminal environment for methanogens. Rarefaction analysis of the sequences in the database indicated that the coverage of the diversity at species level was 65% for archaea in 2011. However, very recently ruminal methanogens accounts about 8623 archaeal sequences of rumen origin (RDP Release 11, update 3). About 90% of these sequences were assigned to methanogens (RDP Release 11, update 3). These sequences are classified onto ten known genera, majority of sequences were under *Methanobrevibacter* followed by *Methanosphaera, Methanomicrobium* and *Methanobacterium*. The order Thermoplasmatales, which was previously referred to as the rumen cluster C (RCC) group, is represented by few sequence of the total archaeal sequences.

Among the sequences in the data bases, eight species of methanogens have been isolated into pure cultures of *Methanobacterium formicicum, Methanobacterium bryantii, Methanobrevibacter ruminantium, Methanobrevibacter millerae, Methanobrevibacter olleyae, Methanomicrobium mobile, Methanoculleus olentangyi, and Methanosarcina barkeri (*McAllister *et al.*, 1996*; Janssen* and Kirs, 2008; Zhou *et al.*, 2008) [26,40,41]. Moreover, in 2013 five new species were isolated, including *Methanobrevibacter boviskoreani* (Korean native cattle) (Lee *et al.* 2013) [42], *Methanobacterium beijingense* (goat), *Methanoculleus marisnigri* (Indian crossbred cattle), *Methanoculleus bourgensis* (Holstein cattle), and *Methanosarcina mazei* (isolated from the rumen of Korean Hanwoo cattle) (RDP database). Besides, one Thermoplasmatales-like pyrrolysine-dependent methanogen was isolated from bovine (GenBank access number: CP002916). Collectively, 16S rRNA gene sequences from cultured methanogens only accounted for 0.7% of the total archaeal sequences of rumen origin. Most of the isolates are members of the family Methanobacteriaceae and several taxa do not have a single cultured representative. Therefore, there are many uncultured species/ strains of methanogens have been isolated with culture independent techniques like 16S rRNA gene clone libraries and DNA sequence analysis (Klieve *et al*. 2009; Ouwerkerk *et al.* 2008; Wright *et al*. 2008). The possible reason might be these species owing to very specific requirements for particular substrates and other physiological conditions.

Genera and species

The majority (92.3%) of archaea are classified into three genera such as *Methanobrevibacter* (61.6%), *Methanomicrobium* (14.9%), as well as a *Methanomassiliicoccales* (15.8%) (Sirohi *et al.* 2010) [43]. Among which *Methanobrevibacter* was the dominant genera of methanogens followed by *Methanosphaera* and *Methanobacterium* in ruminants (Wright *et al.*, 2004, 2008; Nicholson *et al*., 2007; Ouwerkerk *et al*., 2008; Snelling *et al.*, 2014; St-Pierre *et al*., 2015; Zhou *et al* 2017a, 2017b and Wang *et al.* 2017) [44-52]. On the other hand, few reports indicated that the dominant ruminal methanogens belonged to rumen cluster C in dairy cows accounting 71% of the total sequences (Wang *et al*. 2016) [53]. Similarly, in Tibetan ruminants appears to affil¬iate with rumen cluster C or recently *Methanoplasmatales* (Iino *et al.*, 2013 and Huang *et al.*, 2016) [54,55]. This review suggests that there is high range of variation with regards to methanogen species among ruminant species and this attributes to type of feed, species, location of animals, type of primers, isolation techniques used by different scientist are highly variable. Generally, this review summarized that the relative abundance of the methanogens genera and respective species in ruminant are shown in order of importance in Table 1.

Item	References
Methanobrevibactor genera *Methanobrevibactor ruminantium*	Tatsuoka et al. 2004; Wright et al. 2007; Nicholson et al. 2007; wang et al. 2017
Methanobrevibactersmithii, thanobrevibactergottschalkii, *Methanobrevibactermilleraeor ethanobrevibacter thaueri*	Zhou et al. 2009; St-Pierre et al. 2015; Henderson et al. 2015 and Gemma et al. 2015; Huang et al. 2016
Methanosarcina barkeri	McAllister et al. 1996; Moss et al. 2000; Boadi et al. 2004; Ouwerkerk et al. 2008
Methanomicrobium genera *Methanomicrobium mobile*	Lin et al. 1997; Yanagita et al. 2000; Tajima et al. 2001; Regensbogenova et al. 2004; Shin et al. 2004 and Chaudhary and Sirohi 2008;
Ruminant cluster C (RCC) genera *Rumen cluster sppc.*	Tajima et al. 2001;Wright et al. 2006, 2007; Janssen and Kirs 2008;
Methanomassiliicoccales genera *Methanosarcina spp*	Lin et al. 1997; Yanagita et al. 2000; Skillman et al. 2004
Methanosphaera stadtmanae	Sharp et al. 1998 and Wright et al. 2004

Source: 2018 review

Table 1: List of methanogens genera and their respective species

Substrates for methanogens

Majority of rumen archaea use H_2 and CO_2 as main substrates for formation of methane (CH_4). The broad diversity of methanogens in rumen would suggest factors other than H2 and CO_2 in determining structure of the community. Hydrogenotrophic methanogens use CO_2 or acetate as their carbon source and H_2 as main electron donor play a dominant role during methanogenesis. While During formatotrophic methanogenesis, four molecules of formate are oxidized to form CO_2 by formate dehydrogenase (FDH). Members of the order Methanosarcinales (Methanosphaera spp.) and Methanobacteriales have been classified into methylotrophs that use methyl containing compounds such as methanol, methylamines or dimethylsulfide to produce CH_4. Acetate is preferred

substrate for Methanosarcina and Methanosaeta that produce CH_4 via aceticlastic pathway (Liu and Whitman 2008) [56]. During acetoclastic methanogenesis, acetate splits to form carboxyl compounds that become oxidized to CO_2. Methyl groups from CO_2 then enters the hydrogenotrophic pathway to form CH_4. Contribution of methyl groups and acetate as substrates for methanogenesis in rumen is likely to be minimal as methanogens that depend on these conversions for producing CH_4 have a very slow growth rate in vitro, suggesting short retention time exerted by normal rumen conditions would prevent them from thriving (Janssen and Kirs 2008) [26]. Miller (2001) [57] noted that *Methanosphaera spp*., as well as Methanosphara stadtmanae from the human colon and Methanosphara cuniculi isolated from the contents of rabbit rectum, can utilize only methanol with H_2 as substrate for growth unlike other methanogenic archaea. Because, Methanosphara. stadtmanae genome does not contain molybdopterin biosynthesis genes and therefore, it is unable to synthesize active formylmethanofuran dehydro¬genase, which forms formylmetha-nofuran from CO_2 (Fricke *et al*. 2006) [58]. In addition, this archaea also lacks genes for carbon monoxide dehydrogenase/acetyl coenzyme A synthase complex (Fricke *et al.* 2006) [58], which may explain why Methanosphara stadtmanae cannot use acetate as a methanogenic substrate. Methanosphara stadtmanae were identified from captive Sumatran orangutans (Pongo abelii) fecal samples. This animal eats fresh fruit as 50% of its daily diet and degradation of fruit pectin could provide methanol as a methanogenic substrate to Methanosphara stadtmanae to outcompete other methanogenic groups. Methanosphara stadmanae can utilize only methanol with H_2 for CH_4 production, while Methanobrevibactor smithii not only uses CO_2, H_2 and/or formate but also contains enzymes facilitating methanol and ethanol utilization (Samuel *et al*. 2007) [59].

Apart from the above common substrates, phosphatidylcholine is also a compound of the plant membrane materials and is rapidly degraded by rumen microorganisms to liberate choline (Neill *et al*. 1978) [60]. Choline is subsequently degraded to trimethylamine. The methyl groups of trimethylamine and methylamine are converted to CH_4. apart from other *Methanobrevibacter spp*. including Methanobrevibactor ruminantium, Methanosarcina barkeri utilize trimethylamine, dimethylamine, and methylamine as substrates for methanogenesis (Hippe *et al*. 1979; Patterson and Hespell 1979) [61,62]. Patterson and Hespell (1979) revealed that when other substrates are unavailable in the bovine rumen, the presence of methylamine compounds may allow noncompetitive growth of Methanosarcina barkeri.

Methanogenesis pathways

Fermentation of carbohydrates results in accumulation of hydrogen, the removal of which through methanogenesis pathways by methanogens allows microorganisms to degrade substrates continuously and supports the rumen anaerobic fermentation process and this occurs by oxidation of sugars via Embden-Meyerhof-Parnas pathway in bacteria, fungi and protozoa, electron carrying cofactors such as NADH must be reoxidized to NAD+ to allow fermentation to continue (McAllister and Newbold 2008) [63]. Three types of methanogenic metabolic pathways are involved in CH_4 synthesis, namely hydrogenotrophic (reduction of CO_2 coupled to the oxidation of H_2), methylotrophic (conversion of methyl-group containing compounds) and acetoclastic (Rother and Krzycki 2010; Ferry 2011) [64,65].

Hydrogenotrophic pathway is generally recognized as the main pathway to remove hydrogen, through which methanogens can utilize H_2 as electron donor to reduce CO_2 to CH_4. Newly recognized methanogens (e.g., rumen cluster C) use a range of methyl donor compounds and CO_2 for CH_4 production, suggesting that other pathways maybe identified (Poulsen *et al.* 2013) [66]. The draft genome of Candidatus Methanomethylophilus Mx1201, a methanogen isolated from human gut belonging to the rumen cluster C, more recently categorized into the order Methanomassiliicoccales (Dridi *et al.* 2012) [67], contains genes for methylotrophic methanogenesis from methanol and tri-, di- and monomethylamine (Borrel *et al.* 2012) [68]. In artificial systems, such as biogas production facilities, acetate is recognized as an important substrate for methanogens, which refers to as acetoclastic methanogenesis (Weiland 2010) [69]. A comprehensive understanding of the functionality of methanogens and their CH_4 producing pathways may provide insights into effective CH_4 abatement strategies.

Methanogenesis is unique to the methanogens, this ability is due to the presence of three coenzymes (Figure 1), which have not been found in other microorganisms namely, coenzyme M, coenzyme B (Factor B) and CoM-S-S-CoB. All of these coenzymes are involved in various oxidation and reduction processes during CH_4 formation (Baker 1999; Boadi *et al.* 2004) [70,71]. The formation of CH_4 from methanol is similar except that from methanol there is either direct formation of CH_4 through coenzyme M, or by methanol oxidation to CO_2 through a pathway which initially proceeds in the opposite direction to CO_2 reduction pathway, before transfer of the methyl group to coenzyme-M, which is then reduced to CH_4 (Ferry 1993) [72]. Thus, the last step in the formation of CH_4 from all pathways proceeds through coenzyme M which is reduced by the methyl-CoM reductase (mcr) enzyme and a cofactor F430 exclusive to the archaea which acts as a prosthetic group to enzyme mcr (Thauer 1998) [73]. It can thus be concluded that methanogens have highly conserved 16S ribosomal sequences which make them a distinct group from other microorganisms. These unique sequences can thus be targeted to perform culture independent molecular analysis of the methanogens.

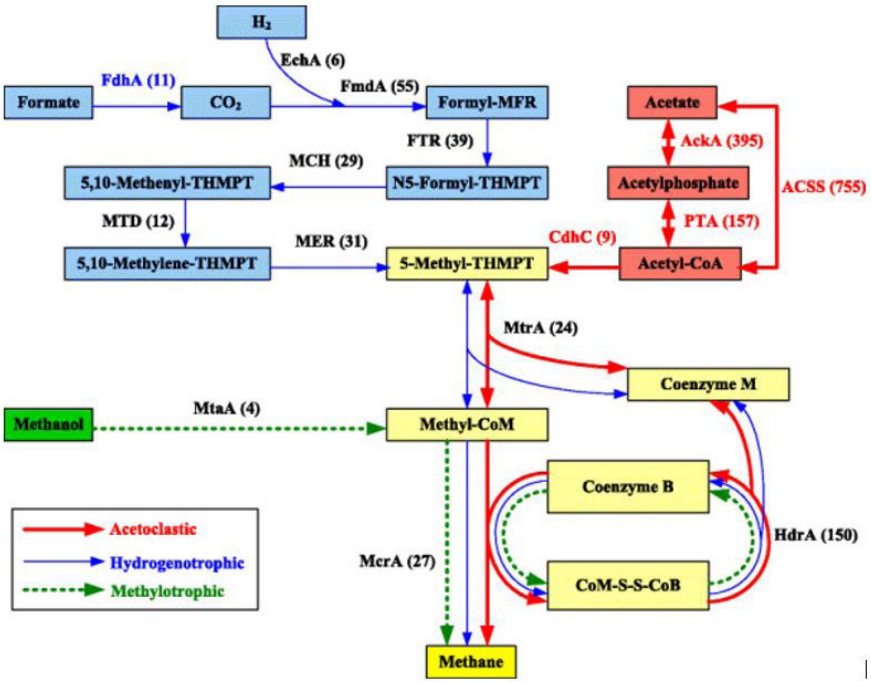

Figure 1: Methanogenesis and role of co-enzymes

It summarizes methanogenesis using the exclusive enzymes mainly coenzyme M which is reduced by an enzyme mcr to produce CH_4 production from all substrates

Association of methanogens and microbes

Associations mainly occur via pools of common metabolites, especially where end products of one group form the substrates of another group. Methanogens interact with other ruminal microbes, including protozoa (Vogels *et al.* 1980) [17], bacteria (Hegarty and Klieve 1999) and fungi (Brul and Stumm 1994) [18,19]. Overall, such interaction benefits rumen fermentation to prevent accumulation of reducing equivalents and inhibition of rumen fermentation and facilitate normal fermentation process in rumen (Kong *et al.* 2013) [74]. Methanogens can associate with fungi, but little is known about fungal-associated methanogens. An early study suggests that rumen fungi do not have endosymbiotic methanogens although they may have ectosymbiotic methanogens (Marvin-Sikkema *et al.* 1992) [75]. In a recent study, species of Methanobrevibacter were detected in cultures of Piromyces, Anaeromyces, and Neo-callimastix (Jin *et al.* 2014) [76]. In addition, methanogens were evident in some rumen fungal cultures, but it was not reported if methanogens and fungi had any type of physical association (Jin *et al.* 2014) [76]. All rumen fungi contain hydrogenosomes and methanogens use H_2 to produce CH_4 (Orpin 1988) [77], but concrete evidence is needed to determine if rumen fungi carry true endosymbiotic methanogens.

A recent study investigated associations between bacteria, archaea, and protozoa, but no strong correlations between archaea and protozoa (Gemma *et al.* 2015) [38], though in earlier study methanogens are known to colonize protozoa, and this mutualistic relationship is believed to enhance CH_4 formation in the rumen (Newbold *et al.* 1995) [78]. Moreover, the occurrence of specific symbiosis between methanogens and rumen cilate protozoa has been speculated on, but till further verification is required (Hackstein 2010) [79]. Lack of strong co-occurrence patterns indicate that these important associations are probably non-specific, or occur at a strain level and, further investigation is required to validate those reports, as mechanisms that mediate the colonization of protozoa by archaea remain to be elucidated. These could have interesting evolutionary aspects if they allow non-specific interactions to form or are mediated by strain-specific mechanisms that confer different partner specificities within archaeal or protozoal species. In addition, lack of strong association patterns between protozoa and major methanogen groups on the other way, suggests that conserved mechanisms may mediate the interactions between H_2 producing and H_2 consuming microbes, allowing flexible interactions. This may aid CH_4 mitigation research, since interfering with these potentially universal mechanisms could slow the rate of H_2 transfer and so slow CH_4 formation (Stams and Plugge 2009) [80].

Cellulolytic bacteria also have association with methanogens, Minato *et al.* (1992) [81] hypothesized that cellulolytic bacteria supply H_2 to methanogens. In line to this, Morgavi *et al.* (2010) [82], noted that integration of methanogens into bacterial biofilms on feed particles itself represents a form of interaction, and most fermentative ruminal bacteria produce CO_2 and H_2, Thus, rumen bacteria and methanogens interact mutualistically through interspecies H_2 transfer. Such interspecies H_2 transfer was demonstrated in co-cultures of methanogens with Ruminococcus albus (Wolin *et al.* 1997) [83], R. flave- faciens (Latham *et al.* 1977) [84] and Selenomonas ruminantium (Scheifinger *et al.* 1975) [85]. Consequently, interaction between rumen bacteria and methanogens affects energy conservation, volatile fatty acid profiles, and CH_4 production by rumen microbiome. On the

other hand, no strong associations were found between most abundant bacteria and archaea (Gemma *et al.* 2015) [38], It was surprising findings, since rumen bacteria degrade feed and produce the substrates for methanogens, mainly H_2 and methyl groups. However, there was positive associations between some less abundant bacteria and archaea, the bacteria were succinate-producing Succinivibrionaceae, succinate-using Dialister, and the amino-acid-fermenting Acidaminococcus, and methanogens related with Methanomassiliicoccaceae, Methanosphaera spps. A4, and Methanobrevibacter boviskoreani. Succinivibrio spps. degrade pectin (Bryant 1956) [86]. Methanomassiliicoccaceae (Paul *et al.* 2012) [87] and Methanosphaera (Miller and Wolin 1985) [88]. Other associations were also between the methylotrophic methanogens Methanosphaera sp. ISO3-F5 and different bacteria, including members of Lachnospiraceae. These associations may be based on the ability of Lachnospiraceae to degrade pectin and so provide methanol as a substrate for methylotrophs (Dehority 1969) [89]. The associations between other Methanomassiliicoccaceae groups and various unclassified members of Bacteroidales also suggest the possibility of yet further methanol-dependent metabolic interactions [90-96].

Conclusion

It might be possible to deduce that with the exception of rare studies, the genera Methanobrevibacter and methanobactrium are considered as the dominant methanogenic group followed by RCC in ruminants. However, methanogen community structure is so dynamic depending on animal and other environmental factors. This review finally, hypothesized that most of the previous studies are focused on methanogen community only in rumen of ruminants focusing with obvious pathway. However, little is known about the distribution of methanogens across the gastro-intestinal tracts of ruminates. Hence, to discover some novel genes, future study is warranted to address the issues to have a complete understanding of methanogens in ruminants. Moreover, methanogen community structure and methane production pathway using format as a substrate is remained to be unknown and future works are needed in addressing these gaps.

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