Molecular analysis of the bacterial microbiome in the rumen of Algerian dromedary

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Keywords

Camelids, digestive tract microflora, natural environment, rumen fluid, Algeria

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Summary

The bacterial community of the forestomach plays important roles in the digestive processes of ruminants and pseudo-ruminants. To investigate the rumen microbiota in the pseudo-rumen of camels (*Camelus dromedarius*) raised in a natural environment in Algeria, bacterial diversity was determined from 25 dromedaries using 16S rRNA gene amplicon sequencing. A total of 25 bacterial phyla were identified across all the samples, including Firmicutes (close to 85%), Bacteroidetes (about 12%) and to a lesser extent Proteobacteria (< 1%), with these three phyla together accounting for more than 97% of all sequences. Our results are consistent with previous observations of bacterial communities diversity and abundancy in the rumen or pseudo-rumen of other ruminant species (either domestic or wild), although the abundance of individual bacterial phyla showed remarkably high disparities. Links between the richness and type of diet and the composition of the rumen microbiome are discussed.

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■ INTRODUCTION

Camels are very hardy animals, which can tolerate a dry climate and extreme temperatures and weather (Sibtain et al., 2010). They can depend on scarce natural forage to cover their nutritional needs because they browse on a wide variety of plants, like thorny bushes, halophytes, and aromatic types, which domestic ruminants mostly avoid (Iqbal and Kha, 2001). Although camels are polygastric animals, they are often referred to as pseudo-ruminants due to some anatomical and physiological differences in their gastric structures when compared to those of true ruminants. In contrast to the latter's four-chamber stomachs, camel stomachs have only three chambers with no omasum (Von Engelhardt et al., 2007). In addition to this anatomical difference, camels retain feed particles in the forestomach for a much longer time than other ruminants (Abbas et al., 1995). Indeed, camels are better adapted to the digestion of poor-quality forage than other ruminants living under the same conditions (Robinson et al., 2006), while cattle have a higher grazing rate and ruminating efficiency than camels (Khana and Zaied, 1991). Forestomaches are rich in microorganisms, the population of which is mainly influenced by the animal's diet (Nguyen Cong et al., 2019). The rumen microbiome is dominated by obligate anaerobic microorganisms originating from all three taxonomic domains of life, i.e. Archaea, Bacteria, and Eukarya. Bacteria are the most abundant microbes in the foregut of ruminant animals, with approximately 10^{11} cells/ml and over 200 species (Gharechahi and Salekdeh, 2018). Few studies have investigated the characteristics of rumen microbiota in camels, especially in natural environments. This study was undertaken to assess the microbial composition and bacterial diversity traits of rumen samples obtained from Algerian camels under pasture conditions.

■ MATERIALS AND METHODS

Animals

The samples were obtained from animals delivered to the abattoir of Tamanrasset for slaughter during the cold months of November and December 2019. The camels originated from arid natural pastures in southern Algeria (Tamanrasset is 1,919 km from Algiers). Animals there are free ranging, feed exclusively on hard wild weeds such as those belonging to the genera *Astragallus*, *Atriplex*, *Artemisia*, and are not supplemented with concentrates. A total of 25 rumen contents

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were sampled. They were taken from animals ranging in age from 10 months to 4 years that were declared healthy after *ante mortem* and *postmortem* veterinary inspections. The camels were opportunistically sampled immediately after slaughtering.

Laboratory Analysis

Using sterile plastic syringes, 200 mL of rumen fluid contents were obtained from each camel during the evisceration of the animals and transported in a frozen airtight container to a field lab within 30 min. The samples were then transferred to 250 mL beakers and the solid and liquid phases were separated using a Bodum coffee filter plunger. Subsamples (5 mL) of the liquid phases of the samples were collected and immediately stored at –80 C. Total DNA was isolated from each rumen sample using QIAGEN Bio Sprint 96 workstation (Valencia, CA, United States). To assess the rumen microbial profiles, the bacterial V1 – V3 region of 16S rRNA genes were amplified using primers as described previously (Nguyen Cong et al., 2019), i.e., for bacteria, the primers were Ba9F (5'-GAGTTTGATCMTGGCTCAG-3') and Ba515Rmod1 (5'-CCGCGGCKGCTGGCAC-3').

Metagenome DNA sequencing was performed at Liege University (Belgium) according to the standard protocols. A library was prepared using a Nextera DNA Library Preparation Kit (Illumina, San Diego, CA, USA) following the manufacturer's protocol.

The high-quality sequences were used in the final analysis. Sequences were clustered into operational taxonomic units (OTUs) using the UCLUST algorithm (97% similarity) in QIIME v.1.8.0.

Differences in alpha diversity and relative abundance of taxa among different groups were analyzed using the Kruskal – Wallis rank-sum test in R.

Pear version 0.9.6 (Nguyen Cong et al., 2019) was used to merge read1 and read2 into a single dataset. A de novo picking of OTUs was performed using SILVA databases as references. Alpha diversity indices and the number of OTUs were calculated using QIIME.

QIIME (QIIME v.1.8.0) was used for 16S rRNA data quality control and analysis. We used the SILVA database (SILVA, Release 119) to analyze taxonomy. The high-quality sequences were used in the final analysis. Sequences were clustered into OTUs using the UCLUST algorithm (97% similarity) in QIIME v.1.8.0.

Statistical Analysis

Means, median and their coefficient of variation for relative abundance of OTUs were calculated. Principal component analysis was performed based on the different phyla observed in the samples.

■ RESULTS AND DISCUSSION

A total of 25 bacterial phyla were identified across all the samples, including Firmicutes (close to 85%), Bacteroidetes (about 12%) and to a lesser extent Proteobacteria (< 1%), with these three phyla together accounting for more than 97% of all sequences (Table I).

We obtained a total of 766,114 high-quality sequences, with between 33,247 and 47,873 valid sequences for each sample. The rarefaction curves for the OTUs detected showed that the number of OTUs increased with the depth of sequencing.

Sequences were classified into 28 phyla, 44 classes, 110 orders, 190 families, and 11,759 genera.

As well as richness and diversity of all phyla were lowest in rumen samples. Furthermore, marked inter-camel variations were not observed in community diversity levels.

Regarding the type of phyla, the ratio of Firmicutes to Bacteroidetes, although largely in favor of the first, was reversed for several animals showing antagonistic proportions between the two phyla.

Our results revealed that Firmicutes and Bacteroidetes were the main phyla in liquid sampled from camel pseudo-rumen. The vectors show the correlation between the main phyla and the two axes. The coordinates of dispersion points were standardized according to the maximum value observed in each axis.

Studies performed on beef and dairy cattle showed that the phylum retrieved most is generally Firmicutes when diets are rich in forage, and Bacteroidetes when diets are rich in cereals (Deusch et al., 2017). Other studies also have recorded that bacterial microbiota is commonly dominated by Firmicutes and Bacteroidetes in the rumen and feces of Bovidae. The phyla of rumen bacteria previously reported by gene sequencing mainly included Bacteroidetes, Firmicutes, Proteobacteria, Spirochaetae, Fibrobacteria, and Actinobacteria (Huws et al., 2007; Pitta et al., 2014a; Zhang et al., 2017; Rabee et al., 2021). The fact that the phylum Firmicutes was by far the predominant phylum in the population of bacterial communities is consistent with Du et al. (2019). This phylum is the main contributor to lignocellulose degradation. In the present survey, the relative abundance of the main phyla of the rumen microbiota may reflect the uniqueness of the camel's diet, which typically includes material with a high lignocellulose content (Gharechahi and Salekdeh, 2018). Ming et al. (2017) also reported that Firmicutes was the predominant phylum in Inner Mongolian cattle, Inner Mongolian domestic Bactrian camels and Mongolian wild Bactrian camels.

The phylum Firmicutes was dominated by the family Ruminococcaceae, which included mainly the genera Ruminococcus, Saccharofermentans, Butyrivibrio, Succiniclasticum, Selenomonas and Streptococcus (Table II). Quite a few species from these genera produce several types of cellulolytic and hemicellulolytic enzymes and

Table 1: The different phyla observed in Algerian camel rumen liquid /// *Les différents phyla observés dans le jus de rumen des chameaux algériens*

Phyla	Mean (%)	CV (%)	Median (%)	CV (%)
Firmicutes	84.51	15	89.87	16
Bacteroidetes	11.95	95	7.90	156
Bacteria_ph	1.00	117	0.56	226
Proteobacteria	0.82	213	0.38	486
Actinobacteria	0.49	68	0.40	86
Patescibacteria	0.48	173	0.17	545
Lentisphaerae	0.16	147	0.04	766
Chloroflexi	0.12	81	0.11	91
Tenericutes	0.11	216	0.05	571
Synergistetes	0.09	124	0.05	277
Spirochaetes	0.06	79	0.05	99
Cyanobacteria	0.04	156	0.02	357
Kiritimatiellaeota	0.04	86	0.03	113
Planctomycetes	0.03	197	0.01	738
Epsilonbacteraeota	0.03	155	0.02	285
Elusimicrobia	0.02	128	0.01	332
Fusobacteria	0.02	276		
Fibrobacteres	0.01	143		
WPS-2	0.01	392		
Verrucomicrobia	0.01	174		
Armatimonadetes	0.03	198		

CV: coefficient of variation /// *CV: coefficient de variation*

Table 2: The main bacterial genera observed in Algerian camel rumen liquid /// *Principaux genres bactériens observés dans le jus de rumen des chameaux algériens*

Main bacteria	%
Acetitomaculum	2.31
Bacteria_ge	0.99
Bacteroidales_UCG-001_ge	0.89
Christensenellaceae_R-7_group	9.68
Clostridiales_ge	2.96
Lachnospiraceae_AC2044_group	3.33
Lachnospiraceae_ge	14.41
Lachnospiraceae_NK3A20_group	1.55
Lachnospiraceae_XPB1014_group	1.53
Lactobacillus	1.77
Others	18.69
Prevotella_1	5.41
Rikenellaceae_RC9_gut_group	3.01
Ruminococcaceae_ge	5.31
Ruminococcaceae_NK4A214_group	12.91
Ruminococcaceae_UCG-010	1.44
Ruminococcaceae_UCG-014	3.11
Ruminococcus_1	2.24
Ruminococcus_2	2.15
Saccharofermentans	1.64
Solibacillus	3.76
Streptococcus	0.89

degrade hemicellulose, pectin, and cellulose present in plant cell walls (Rabee et al., 2021). The phylum Bacteroidetes is widely distributed in the environment, including in soil, sediments, sea water, and the gut and skin of animals. They are normally mutualistic, making up the most substantial portion of the mammalian gastrointestinal microbiota, where they play a key role in processing complex molecules into simpler ones in the host's intestines (Ming et al., 2017; Xu et al., 2017). Bacteroidetes were abundant in the Inner Mongolian domestic Bactrian camels and Mongolian wild Bactrian camel populations (4.05% and 4.52%, respectively), which agrees with the present results. Bacteroidetes can use simple sugars when available; however, the main sources of energy for Bacteroidetes species in the gut are plant glycans (Martens et al., 2008). Moreover, Bhat et al. (2013) reported that the members of the phylum Bacteroidetes degrade a wide range of substrates, including cellulose, pectin and soluble polysaccharides, and unclassified Bacteroidetes are more specialized in lignocellulose degradation. In the present study, all members of the phylum Bacteroidetes were assigned to the family Prevotellaceae and the genus Prevotella, which agrees with other studies (Berman et al., 2020). The genus Prevotella includes bacteria which degrade different substrates, including hemicellulose, pectin, proteins and peptides. In ruminant rumen, *Prevotella* was found to contain many genes coding for enzymes (Betancur-Murillo et al., 2023), and it can break down a variety of polysaccharides (Chen et al., 2017)**.** Although *Proteobacteria* is a diverse phylum and includes a wide variety of pathogens, it is an important phylum in rumen metabolism (Madigan and Martinko, 2005). It tends to become co-dominant in ruminants fed starch-based or high concentrate diets (Pitta et al., 2014b; Zhu et al., 2016). Gharechahi and Salekdeh (2018) revealed that the microbial community of camel rumen was not dominated by species belonging to *Proteobacteria* (4.1%). Our results showed that the phyla Actinobacteria, Patescibacteria, Lentisphaerae, Chloroflexi and Tenericutes accounted for proportions ranging from 0.5 down to 0.1%. Actinobacteria are a significant and interesting group of gram-positive bacteria. They are regular, though infrequent, members of the microbial life in the rumen, and represent up to 3% of total rumen bacteria from cows and sheep (Šuľák et al., 2012). In camels, at 2 months of age, the fecal microbiota is composed of Firmicutes, Proteobacteria, and Actinobacteria (He et al., 2019). The Actinobacteria phylum has acetogenic activities and was also found in the rumen of moose (Ishaq et al., 2015). Hinsu et al. (2021) and Rabee et al. (2021) reported that phyla that were detected to be less than 0.8% were Actinobacteria, Chloroflexi, Lentisphaerae, and Tenericutes (Hinsu et al., 2021; Rabee et al., 2021). The latter phylum was reported to be the most predominant phyla in wild sika deer. The phylum Tenericutes, class Mollicutes previously were rarely found in gastrointestinal tracts and were identified for the first time in wild chimpanzee (McLaughlin et al., 2012). Moreover, Tenericutes were discovered extensively in both carnivorous and herbivorous mammals, such as sables and cows (Guan et al., 2016), and in aquatic animals, like the Yangtze finless porpoise (McLaughlin et al., 2012). Ming et al. (2017) reported that Verrucomicrobia was the second most predominant phylum in Inner Mongolian cattle, Inner Mongolian domestic Bactrian camels and Mongolian wild Bactrian camels (Ming et al., 2017). In the present study, Verrucomicrobia was retrieved very little, and it should be noted that 1% of Bacteria phyla were listed as unclassified. Overall, the present results could be interesting to consider given that the animals studied were raised in the wild. Many studies undertaken over the past few decades have investigated the factors that could affect the rumen microbiota, including host species, age, health status, geographical location, and weather (Carberry et al., 2012). Diet is a key factor in shaping the gut microbiota. In the wild, the camel's diet is dominated by a variety of woody shrubs and tree biomasses, along with various halophytes, species which are not favored by most ruminants (Gharechahi et al., 2015; Samsudin et al., 2012). Consequently, their rumen microbes should have the capacity to degrade feedstuffs that are rich in lignocellulosic materials. It is well recognized that species belonging to the phyla Bacteroidetes, Firmicutes and Fibrobacter are major agents of lignocellulose degradation in the rumen (Flint et al., 2008; Jose et al., 2017). There are few similar feeding situations with respect to true ruminants. Wild ruminants could be viewed as points of comparison. Microbial composition varied across samples in Oryx Damah (Shang et al., 2019). According to Guan et al. (2017), Firmicutes, Bacteroidetes and Tenericutes were the predominant phyla in wild sika deer, while in captive animals, the same authors found that the Firmicutes proportion decreased, the Bacteroidetes proportion increased and that of Proteobacteria reached values close to 5% (Guan et al., 2017). Qin et al. (2020) reported that in the goitered gazelle (*Gazella subgutturosa*), a total of 25 phyla were found, of which the dominant phyla were Firmicutes and Bacteroidetes in both summer and winter, representing more than 90% of the overall relative abundance (Qin et al., 2020). Our results are thus consistent with these previous observations, although the abundance of individual phyla showed remarkably high disparities. This study has some limitations, including the relatively small sample size and an inability to control for potentially important variables such as sex and age.

■ CONCLUSION

This study is the first to describe the characteristics of the microbial communities of dromedaries raised on natural pasture in arid regions. Our results revealed that Firmicutes and Bacteroidetes were the main phyla in liquid sampled from the camels. The dominant bacterial genera were *Prevotella*, *Ruminococcus*, and *Butyrivibrio*. The composition of the microbial community in the camel rumen is similar to that of other ruminants with differences in the abundance. The structure of the microbial communities was as expected from camels fed in a poor environment, but a large variability exists between individual animals.

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Conflict of interest

The authors declare no conflict of interests.

Statements of author contributions

NS: Conceptualization, Writing. RB methodology, investigation. AF: Investigation. BT: Review, visualization. JLH: Resources, review and conceptualization.

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Résumé

Sahraoui N., Boukert R., Fertoul A., Taminiau B., Hornick J.L. Analyse moléculaire du microbiome bactérien dans le rumen du dromadaire algérien

Les communautés bactériennes des pré-estomacs, notamment le rumen, jouent un rôle important dans les processus digestifs des ruminants et des pseudo-ruminants. Pour étudier le microbiote du rumen dans le pseudo-rumen de camélidés (*Camelus dromedarius*) élevés dans un environnement naturel en Algérie, la diversité bactérienne a été déterminée chez 25 dromadaires en utilisant le séquençage de l'amplicon du gène de l'ARNr 16S. Un total de 25 phyla bactériens a été identifié sur l'ensemble des échantillons, dont les Firmicutes (près de 85 %), les Bacteroidetes (environ 12 %) et, dans une moindre mesure, les Proteobacteria (< 1 %), ces trois phyla représentant ensemble plus de 97 % de la totalité des séquences analysées. Nos résultats sont cohérents avec les observations antérieures de la diversité et de l'abondance des communautés bactériennes dans le rumen ou le pseudo-rumen d'autres espèces de ruminants (domestiques ou sauvages), bien que l'abondance des phyla bactériens individuels ait montré des disparités remarquablement élevées. Les liens entre la richesse et le type de régime alimentaire et la composition du microbiome du rumen sont discutés.

Mots-clés : Camélidés, microflore du tube digestif, environnement naturel, fluide du rumen, Algérie

Resumen

Sahraoui N., Boukert R., Fertoul A., Taminiau B., Hornick J.L. Análisis molecular del microbioma bacteriano del rumen de dromedarios argelinos

Las comunidades bacterianas de los preestómagos, especialmente el rumen, juegan un papel importante en los procesos digestivos de los rumiantes y los seudorrumiantes. Para estudiar la microbiota del rumen en el seudorrumen de los camélidos (*Camelus dromedarius*) criados en un ambiente natural en Argelia, se determinó la diversidad bacteriana en 25 dromedarios utilizando la secuenciación del amplicón del gen del ARNr 16S. En el conjunto de muestras se identificó un total de 25 filums bacterianos, entre los cuales: Firmicutes (cerca del 85 %), Bacteroidetes (aproximadamente el 12 %) y, en menor medida, Proteobacteria (< 1 %). El conjunto de estos tres filums representa más del 97 % del total de las secuencias analizadas. Nuestros resultados son coherentes con las observaciones anteriores de diversidad y abundancia de las comunidades bacterianas en el rumen o el seudorrumen de otras especies de rumiantes (domésticos o salvajes). Sin embargo, la abundancia de los filums bacterianos individuales se ha mostrado notablemente dispar. En el artículo se discute la relación entre riqueza y tipo de régimen alimenticio, y composición del microbioma del rumen.

Palabras clave: Camélidos, microflora del tracto digestive, ambiente natural, fluido del rumen, Argelia