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Rumen microbial genomics: from cells to genes (and back to cells)

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Abstract

The rumen harbours countless bacteria, archaea, ciliated protozoa, fungi, and viruses: various microorganisms that have established multiplicity of relationships to efficiently digest complex plant fibres and polysaccharides to produce volatile fatty acids (VFAs), microbial proteins, and vitamins, essentials for the host’s health, growth and performances. Recent studies using omics-based techniques have revealed that changes in rumen microbiota are associated with changes in ruminants’ production and health parameters such as feed efficiency, methane yield, milk composition and ruminal acidity. However, traditionally, rumen microbes were unveiled using anaerobic culture-based techniques, which are at the origin of most of the basic concepts and understanding of the rumen functioning. Isolating and culturing microbes is frequently more difficult, time-consuming and requires more training than molecular techniques, which explains why culture seems to be abandoned in favour of sequencing. Microbial cultures enable the study of substrate preferences and product output, essential growth requirements, biocide production, and susceptibilities; obtaining a pure culture also enables genome sequencing of these strains. We propose here, after a brief report of published rumen isolates, a comprehensive review of current advances in molecular methods to identify novel rumen microbes and discuss how culturing and mathematics could enhance our understanding of rumen microbiology.

Key words: ruminants, microbiota, pure cultures, modelling, genomics

Review methodology

This review is reported under the PRISMA 2020 guidelines for a systematic review. We conducted a comprehensive Web of Science search, using search terms "rumen" and "isolate" spanning the period 1945-2022 for an overview of
culture-based studies exploring rumen microbiota. Further, we searched academic databases (PubMed, Scopus, Web of Science) to identify articles reporting enhanced genomic and mathematic evaluation of rumen microbiota.

Introduction

Ruminant livestock systems make both positive and negative contributions to the development of sustainable agriculture. Ruminants convert roughages into high-quality proteins for human consumption while adding value to poor or erodable lands. At the same time, ruminant production is criticised for its negative impact on the environment and feeds that can be used for human consumption. Under the menace of climate change, ruminants face the challenges of feed scarcity, reduced productivity and increased health burden.

Ruminants have adapted their digestive systems to eat only plants, and they are most efficient to retrieve energy from the plant cell walls than monogastric herbivores. Their stomach has four separate compartments with a distinctive function, allowing them to digest without thoroughly chewing. The partially chewed plant material is further processed by microbes in the rumen section of the stomach. Microbes break down organic matter and ferment it to produce volatile fatty acids, the ruminants' primary energy source. Rumen microorganisms have a critical role in ruminant nutrition and health, but, on the downside, they generate methane – a potent greenhouse gas and contribute to ammonia emissions. Research in rumen microbiota started with the pioneering work of Robert Edward Hungate more than 50 years ago [1, 2]; the growing evidence of the importance of rumen microbes for sustainable livestock brought researchers to consolidate efforts in 2011 by forming The Rumen Microbial Genomics Network. The network serves as a global collaborative platform for researchers, employing microbial genomics methodologies to understand the rumen microbiome better to address global agricultural concerns. Several international projects underpin the network: Hungate 1000 [3, 4], Global Rumen Census [5], RuminOmics [6, 7], RumenPredict [8], MASTER, and HoloRuminant. These projects contributed to our enhanced comprehension of the rumen microbial ecosystem.

The rumen contains representatives of all domains of life: Bacteria, Archaea, Eucarya. Bacteria are the most abundant and diverse; however, a diverse range of protozoa can also be found. Anaerobic fungi are also widely distributed, and bacteriophages are integral to the microbiota. Archaea are the only group producing methane. Numerous reviews address the composition of rumen microbiota in different ruminant species and at different physiological stages [4, 6-12], with the main focus being on Bacteria and Archaea as of their implication in feed digestion and methane production. But scientists agree that gaps of knowledge remain. This review stresses the limited understanding of individual microbes, as specific species could be the key to improving the sustainability of ruminant production systems. We also discuss research challenges to improve rumen microbial understanding, including opportunities for developing enhanced predictive models of rumen metabolism.

Cultured rumen microbes
In 1959 [13] and later in 1964 [14], it was suggested that most of the functionally important bacterial groups had already been described. Rumen bacteria (and archaea — classified at the time within bacteria) were initially classified according to specific wall staining tests into Gram-negative or Gram-positive species and their ability to grow on certain substrates or produce specific metabolites. Hungate [15] proposed to divide them into cellulolytic, amylolytic, hemicellulolytic, saccharolytic, proteolytic, methanogenic, lipolytic, and bacteria that use the products formed by other microbes. This classification was recently brought back in the spotlight by the proposal of the functional group concept [16], dividing microorganisms into groups based on metabolic inputs and outputs and irrespective of the taxonomy. However, this implies that an in-depth knowledge of microbial physiology is accumulated. The time and effort required to isolate and identify pure rumen microbes in cultures preclude this technique as a tool for cataloguing the complex rumen microbiota; still, the culture of isolates alone or in defined mixtures remain essential for the understanding of critical mechanistic factors governing microbial functionning. Through the growth of pure cultures under conditions similar to those of the rumen, it is possible to infer information on the role of these strains in their complex natural environment. This information derived from pure culture alone or simplified combinations can be used to formulate a hypothesis to be tested in the diverse community of the rumen.

In this context, we conducted a systematic literature survey for microbial isolates from the rumen (Table1). The survey was performed in Web of Science (WoS) (accessed January 2022) with the search terms "rumen" and "isolate", spanning 1945-2022. We examined the resultant titles, abstracts, and full-text for relevance to the topic and extracted the relevant information from each study. However, the WoS search missed some important documents. Therefore, we reviewed the cited references in all relevant publications and journal articles not listed in WoS and extra references known to the authors. In addition, we included all ruminant animal species but excluded isolates from faecal contents.

Following the development of anaerobic techniques for the culture of strictly anaerobic bacteria in the 1950s [17], a renewed interest can be observed in the isolation of representative rumen microbes from the beginning of the 90s (Figure 1). Most of the studies included in the survey employed the classical "most probable number" [18] or the "roll-tube method" developed by R.E. Hungate [19]. In our survey, we counted more than 14 000 isolates. More than 80% of the articles and the large majority of the isolates were Bacteria (Figure 2), anaerobic fungi of the Neocallimastigomycota phylum were the second most reported (348 isolates). In addition, we enumerated 25 Archaea strains, 18 bacteriophages isolated from rumen contents and 15 protozoa.

The most frequently studied bacterial strains belong to the Firmicutes phylum, 22% of all isolates (15% were lactic acid bacteria characterised only by phenotypic screening), Fibrobacter far behind, represented 0.3%. The large majority, 65%, of the bacterial strains remained unclassified compared to only 0.4% of isolated fungi. This can be easily explained by the research strategy adopted in papers reporting many initial bacterial isolates. These pure strains were further screened for relevant phenotypic properties, as enhanced fibre degradation activity, detoxification potential (mainly tannins metabolism), fatty acids metabolism (mainly CLA-related), lactic acid
production or consumption or acetogenesis; from this initial screening, only the best performers were retained and
further characterised morphologically and taxonomically. Regrettfully, non-selected isolates have probably been lost,
and the selected strains’ fate is also uncertain. In addition, not all the isolated strains in “rumen” labs worldwide have
been mentioned in publications, and many strains may still reside in freezers. Nevertheless, such a large panel of
deeply characterised microbes constitutes an excellent point of departure for exploring fundamental microbial
interactions. To improve our understanding of cultured rumen microbes, in 2011, the Hungate1000 project was
launched. Coordinated and led by the RMG network, this initiative aimed at generating a reference set of 1000
microbial genomes cultivated from various ruminant host species [3, 4]. At that time, only 14 bacteria and one
methanogen from the rumen had their genomes sequenced. The project so far has produced more than 500
sequenced genomes, constituting the Hungate genome catalogue [3] (480 are bacterial, 21 are Archaea and 7
Viruses). Additionally, 221 cultured genomes were produced within independent studies [12].

As for the identified isolates, the Hungate1000 database is dominated by bacteria from the Firmicutes
phylum, while Bacteroidetes members are under-represented (Figure 3) [3]. Additionally, there is only one
Fibrobacteres-related strain, *Fibrobacter succinogenes* HM2, while in our survey, we numbered more than 50 strains
isolated from bovine or sheep rumen, 38 of them having already their genomes sequenced [20]. *F. succinogenes* is a
remarkably proficient fibre degrading bacterium whose enzymatic system has been extensively studied [20-24]. *F.
succinogenes* S85 has been shown as an excellent model for exploring the species’ fibrolytic traits, as the strain has
preserved its enzymatic characteristics compared to numerous phylogenetically close isolates [23]. In a comparative
pure culture assay, *F. succinogenes* strains S85 and A3C digested more cellulose than the other two prominent
rumen cellulolytic bacteria: *Ruminococcus albus* and *R. flavefaciens* [25]. Furthermore, a recent in vivo work
showed that *F. succinogenes* S85 was outcompeted by *Ruminococcus* strains in gnotobiotic model lambs [26].

However, the authors noticed a significant decrease in *F. succinogenes* numbers and transcriptional activity using
classical microbiological tools and high throughput sequencing techniques and highlighted different enzymatic
strategies for cellulose degradation. This work was built on previously whole sequenced genomes and the
characterisation, using pure cultures, of genes essential to fibre digestion. Therefore, it remains decidedly clear that
the pure culture approach generates valuable data for precise phylogenetic and phenotypic characterisation of rumen
microbes and for exploring microbial interaction in fully-controlled conditions.

The Hungate collection is far from complete [3]. However, in a comparative study based on the 16S rRNA
gene sequences, the authors estimated that the Hungate dataset covered 75% of the microbial genera retrieved in the
rumen [3]. This is a pretty good achievement regarding that the estimated percentage of rumen prokaryotes that can
be cultured is only 40% [27]. Despite that, Zehavi et al. noticed that less than 4% of their isolates were represented
in the Hungate collection in their considerable isolation effort. In this regard, pursuing the isolation of rumen
microbes for enriching culture collections is a challenge in the domain. Culture collections are critical for the
conservation and long term utilisation of biological resources; they also support research by supplying biological
material. High throughput culturomics approaches could help isolate new bacteria belonging to the rare biosphere or
poorly represented taxa [27].
Metaxonomics of rumen microbes

Amplicon sequencing of the 16S rRNA gene is the most widely used approach to study rumen microbiota. However, scientists employed various primers (targeting variable regions V1, V3, V4, V5) and assigned taxonomy using various databases (GreenGenes, Ribosomal Database Project (RDP), SILVA), and various pipelines (mothur, QIIME, DADA2 …). In 2018, Denman et al. reviewed the limitations of these techniques, from the primer selection through the sequencing error removal and the OTU-clustering step to the accuracy of the databases for taxonomic affiliation. They argued that some of the weaknesses could be explained by the incorrect use of bioinformatics tools. Redoubling our efforts with a more precise application of these technologies will result in a complete and deep understanding of rumen microbes’ compositional and functional capability [28]. The response was not long in coming, as since several research groups undertook the assessment of protocols for sample processing [29] and data analysis [30, 31]. Establishing standard operating procedures for analysing rumen microbiota is also embedded in collaborative projects such as RumenPredict, MASTER, HoloRuminant. A guide for database choice in rumen amplicon studies [31] employed a rumen-specific reference standard to compare 16S rRNA database classifications. This rumen reference standard comprised 16 bacterial and archaeal full-length 16S rRNA and 9 protozoal 18S rRNA, and libraries were prepared following a previously described sample preparation guide [29] with primers targeting the V4 region [32]. Taxonomic classification was performed against RDP (version 11.5), the Genome Taxonomy Database (GTDB; release date 20/11/2018), SILVA (version 132) and RefSeq + RDP (release date 14/05/2018); the latter two giving the more accurate classification at the genus level.

Meanwhile, amplicon sequencing enriched our knowledge of rumen microbial diversity. A meta-analysis of curated 16S rRNA gene sequences showed that Firmicutes, Bacteroidetes and Proteobacteria are the dominant phyla (93% of all sequences) out of 19 detected [33]. For Archaea, the Methanobacteria were the most abundant. The Rumen Microbial Census network conducted an extensive investigation of the rumen microbial community (742 samples from 32 ruminant species from 35 countries) to identify the core microbiota and elucidate variations in the rumen microbiome linked to ruminant species, diet, and geographical location [5]. This large scale survey confirmed the crucial role of the diet in shaping rumen microbial profile, undoubtedly explained by the amount, physical and chemical nature of feeds supplied.

On the other hand, the diet did not affect the methanogens population, with Methanobrevibacter gottschalkii and Methanobrevibacter ruminantium nearly ubiquitous and representing 74% of the archael sequences [5]. This complies with the ecological niche that methanogens occupy in the rumen as they use fermentation end products from other microbial species as an energy source. Reports on fungal and protozoal metataxonomy are more occasional. Neocallimastigomycota actively take part in the plant biomass degradation ingested by the host animal and their divergence time concorded with the shift of ancestral mammals from primarily insectivory to herbivory [34]. Morphological features and complex life cycle have entangle taxonomic classification of anaerobic fungi, but the use of marker genes made this task easier [35]. Kittelmann et al. [36, 37] used the internal transcribed spacer (ITS1) as a taxonomic marker for describing the fungal community in New Zealand ruminants. Neocallimastix, Piromyces and Orpinomyces accounted for 60% of the detected genera, 24% belonging
to novel clades. However, they highlighted that inter-animal variations are as high as 88%, pointing to the strong effect of the host and the diet. The high variations in ITS1 size and sequence questioned its accuracy [38, 39]; the potential of the large 28S rRNA subunit as a phylogenetic marker has also been explored [40].

Microbial profiling using the 16S rRNA amplicon approach provided valuable insights into the rumen ecosystem composition and its relationship with diet, feed efficiency, enteric methane emissions, milk quality, acidosis or its establishment in early life [6-8, 10, 28, 41-43]. A significant step forward in understanding the influence of microbial community structure on animal phenotype was achieved by identifying ruminotypes associated with methane emissions. Three independent studies, one in sheep [44] and two in dairy cattle [45, 46], established the link between high-methane production and species belonging to Ruminococcaceae, Christensenellaceae and Lachnospiraceae. At the same time, low methane emissions ruminotype had higher relative abundances of succinate producing bacteria [44-46]. More specifically, Ramayo-Caldas et al. highlighted that an OTU classified as Succinivibrionaceae_UCG-001 was only present in low emitting cows. In another study, the same OTU increased in abundance after calving, and authors linked it to the observed enhanced fermentations [47]. The abundance of Succinivibrionaceae-family was also positively associated with propionate concentrations, feed efficiency [48] and milk protein [49]. Furthermore, strong positive and negative interactions at the transcripional level were reported between Succinivibrionaceae and other major bacterial and archaeal taxa from the rumen [50]. All of the above studies support the idea that Succinivibrionaceae members play an essential role in the rumen due to their ecological and metabolic functions. However, the Hungate genome catalogue has only two strains from the Succinivibrionaceae family (Ruminobacter amylophilus and Ruminobacter sp. RM87), and in our survey of cultured isolates, we found only one old article reporting the isolation of 7 Succinivibrio strains [51]. The need arises to isolate more representatives of this taxon. The road is almost paved, as using binned metagenomic data and metabolic predictions, Pope et al. in 2011 designed a defined medium for the for the culture of a Succinivibrionaceae sp. that until then could not be grown axenically in the laboratory [52].

Rumen Uncultured Genomes

The amplicon sequencing approach requires prior knowledge for the design of primers and taxonomic affiliation, but accumulated data in this field made it a highly discerning tool for the phylogenetic description of microbial environmental samples [53]. Nevertheless, functional diversity cannot be directly predicted from phylogenetic diversity in microbial communities. Arguably, the emergence and expansion of metagenomics have been one of the most impressive achievements in microbial ecology during the last decade. Metagenomics refers to the study of genomic material found in environmental samples and offers access to the functional gene content of microbial communities, providing a considerably more comprehensive description than metataxonomics. A significant breakthrough of metagenomics is building metagenomic assembled genomes (MAGs). In this approach, sequences are assembled into scaffolds, which are subsequently categorised into potential MAGs based on tetranucleotide frequencies, abundances, related marker genes, taxonomic alignments, and codon use [54]. In doing so, we can identify novel species and get an insight into their contribution to microbial ecosystem dynamics.
Since 2011 with the first report of 446 rumen genome bins (and 15 draft genomes) [55], thousands of novel MAGs were announced (251 by Parks et al. [56], 99 by Svartstrom et al. [57], 79 by Solden et al. [58], 5845 by Stewart et al. [59, 60], 324 by Li et al. [61], 1200 by Wilkinson et al. [62], 391 by Glendinning et al. [63], 2809 by Anderson & Fernando [64], 4960 in buffalos by Tong et al. [65], 719 by Peng et al. [66], 10373 by Xie et al. [12] around the whole gastrointestinal tract and the list is not exhaustive). Close to 34 000 rumen MAGs were retrieved from ten publicly available datasets [67]; 63% were seen in only one of the datasets, and no MAG was common in all datasets. In this work, the author stressed the need to have standardized procedures for MAGs and corresponding metadata description and a common repository for sharing data. This is a sensible comment which complies with the collaborative efforts of the Hungate1000 project and the SOP for metataxonomic analysis for standardized databases and tools for ruminants gut microbiota analysis.

In some of the studies mentioned above, authors mapped the retrieved MAGs to the Hungate1000 genome database. Li et al. [61] reported a mapping rate of 5.4% (similarity ≥ 95%); 3% of the MAGs from Stewart et al. [60] had ≥ 95% protein identity with Hungate genomes, and this figure increased to 5.4% for similarity rates ≥90%; 3.5% of the MAGs from Anderson & Fernando [64] had a similarity rate ≥95% with genomes from the Hungate1000 database. Only eighteen from the 719 high-quality MAGs in Peng et al. [66] were classified as eukaryotes and identified to belong to the fungal subphylum Neocallimastigomycota. Anyway, though this was the first report of rumen fungal MAGs, the authors underlined that these MAGs are only 73% complete. Indeed, it is particularly challenging to reconstruct eukaryotic genomes because of their size (>10 Mbp) and the presence of frequent repeat region with high GC content. Zehavi et al. [27] accentuated that sequencing approaches (metataxonomics was used in their study) target mainly abundant microbes. In contrast, culture can recover abundant and rare microbes, as the ability to culture a microbe does on intrinsic characteristics and not on their abundance [68]. Though this could partially explain the low coverage of the Hungate database by MAGs, the question of whether these are real microbial species remains. In human faecal samples, MAGs recovered only 77% of the core genes (shared by more than 90% of the present microbial species) and 50% of the variable genes (presents in more than 10%, but less than 90% of the population members) [69]. Moreover, human gut MAGs were shown to be systematically depleted for genes encoding essential functions supporting life [70]. MAGs produced from short-read metagenomic datasets do seldom contain 16S genes. The use of long reads sequencing platforms will bridge the gap between MAGs and cultured species, also with metataxonomics and function. Notwithstanding, to confirm the real biological existence of MAGs, returning to culturing seems necessary. This was already done with the Succinivibrionaceae isolate of the wallaby [52], where the genome reconstruction allowed designing appropriate culture media. Genomic analysis is particularly good at identifying genes and determining the functional relationships between microbes. For validating phenotypic predictions based on genetic data, detecting novel microbes, and investigating microbial interactions with precision, culture-based approaches are still required.

An alternative strategy to offset culture limitation is to isolate individual cells from fresh rumen contents as this was recently done for rumen ciliates [71]. Cells were selected based on morphological traits using electron microscope and subjected to whole genome sequencing using multiple displacement amplification or whole transcriptome
amplification. The analysis yielded 52 high quality ciliate genomes and allowed the classification of 22
morphospecies in 13 genera and the of a new family Dasytrichidae [71].

**Integrating culture-based approaches into the next generation models of the rumen microbiome**

Rumen modelling started in the 70s with empirical and mechanistic developments [72]. Mechanistic rumen models have been consolidated in four modelling structures, namely Molly [73], CNCPS [74], COWPOLL [75] and Karoline [76], which have been incrementally improved over the years. However, the accuracy power to predict the rumen fermentation profile can still be ameliorated [77] by including improvements on physiological components (e.g., VFA absorption) [78], on rumen microbiota representation [79, 80], and the incorporation of thermodynamic, regulation and inhibition factors [81-85].

Kinetic modelling approaches are traditionally used for modelling microbial ecosystems. They are derived from mass-balance principles and have two sets of components: the first defining the mathematical functions representing the kinetic rates of substrate utilization and product formation, and the second containing the parameters that represent the stoichiometry of the reactions. Thus, incorporating data from pure-culture growth experiments in kinetic models detect key parameters, such as the maximal growth rate and the substrate affinity constants, and give insights on ecological properties such as microbial coexistence and exclusion. For example, in work with rumen methanogens, a kinetic modelling approach quantified the metabolic and energetic differences between three species, but the kinetic parameters alone did not explain microbial coexistence. Indeed, adhesion properties played a role in the ecology of methanogens in the rumen [86]. Current rumen fermentation models are in the category of kinetic models. In these models, the rumen microbiota is represented by macroscopic functional groups derived from the study of the main reactions documented in the rumen literature. This representation is then subjected to the modeller's choice and does not integrate data on microbial genomic knowledge.

Alternatively, genome-scale metabolic models (GEMs) allow the integration of microbial genomic information. The core of a GEM of a microorganism is a graph that links the metabolites and biochemical reactions that the organism can perform based on its genetic potential. This graph translates into a stoichiometry matrix of the metabolism. The stoichiometry matrix results from a metabolic reconstruction based on annotation, orthology, gap-filling, and manual curation [87] of the sequenced genome based on a large set of databases and toolboxes (KEGG [88], MetaCyc [89], BiGG [90], Pathway Tools [91], CarveMe [92], KBase [93] and AuReMe [94]). While models of the human gut microbiota already incorporate microbial genomic knowledge [95], genome-scale modelling of the rumen microbiota is at an infant stage [96, 97]. Recently, the GEM approach was used to investigate the interactions between dominant rumen microbial species and their associated phages. Individual GEMs of *Ruminococcus flavefaciens*, *Prevotella ruminicola*, and *M. gottschalkii* were constructed and integrated into a community model using multi-level mathematical frameworks [97]. The model predicted previously unknown interactions among the community members and the complementing role of viral genes in these interactions. In addition, the GEM of a
rumen bacterium involved in lactate metabolism, *Megasphaera elsdenii*, highlighted the high number of metabolic pathways for the production of VFAs [98, 99]. GEMS are often large networks with thousand metabolites and reactions. For example, our preliminary reconstruction study on *F. succinogenes* S85 (Fakhī et al. 2021) resulted in a network with 1567 metabolic reactions and 1588 metabolites.

The next generation of rumen models should build on straightened microbial knowledge, but the systemic understanding of microbial interactions and ruminal fermentation is still lacking. Therefore, *in vitro* culture systems (batch and continuous) are valuable tools to study rumen metabolism, despite their limitations to mimic the rumen ecosystem fully. These mini-consortia are suited for constructing tractable mathematical models with identifiable properties (see, e.g., [101] for a discussion on parameter identifiability). For studying the rumen ecosystem, mini-consortia can be built by selecting microbial species covering the major rumen metabolic cascades [3, 16]. Species selection can be performed from microbial expert knowledge or synthetic ecology approaches targeting specific metabolic functions or microbial interactions [102, 103].

Moreover, species selection can be performed using Metage2Metabo (M2M) [96]. M2M identifies mini-consortia by reconstructing draft GEMs of all members of a microbial community, followed by the identification of the individual and community metabolic potentials, the determination of the cooperation potential (set of metabolites whose production only occur via microbial cooperation), and finally, outputs minimal communities and identifies key species. The originality of M2M is its capability for handling hundreds of genomes and MAGs. M2M was applied to 913 rumen MAGs of the cow rumen [59] and highlighted 127 key species, consisting of 20 essential symbionts and 107 alternative ones [96].

The construction of metabolic networks of key rumen species is an excellent resource for studying the rumen microbial ecosystem via constraint-based reconstruction and analysis (COBRA) methods. COBRA approaches overcome the need to define kinetic rates and their parameters by assuming that internal metabolism operates at steady-state conditions. Genome information and COBRA methods provide analytical tools for (1) assisting the design of cultivation media allowing the study of uncultured gut bacteria [52], (2) designing strategies targeting the inhibition of methanogens in genome-sequenced rumen microbes such as *M. ruminantium* [104], (3) selecting probiotics to enhance rumen function and (4) enhancing our understanding on the robustness of the rumen ecosystem linked to its resilience and functional redundancy [105].

Modelling the rumen microbial ecosystem shares similar challenges to those discussed by [95] and [103] to model human gut microbiota. GEMS are often large networks with thousand metabolites and reactions. Model reductions are needed to construct dynamic parsimonious metabolic models of key rumen microbes within mini-consortia. Individual GEMs can be reduced using dedicated algorithms [106, 107] and exploit transcriptomic data to select active pathways. Reduced GEMs can be further decomposed into their elementary flux modes (EFMs) [108] to derive macroscopic reactions of the rumen fermentation, as it has been in studies on microalgae and yeast metabolism [109, 110]. Rumen modelling can then capitalize on the advances done in other ecosystems (e.g., human...
gut, engineering reactors). Finally, interdisciplinary research is paramount to get the most out of metabolic models and culture systems, implying rumen microbiologists, computational biologists, and mathematical modellers.

**Conclusion**

Advances in next-generation sequencing technologies coupled with sophisticated metagenomics and phylogenetic methodologies have radically altered our perceptions of microbial diversity. However, our inability to cultivate representatives for many newly identified lineages contrasts with the rapid expansion of genomic data, which has led to a better knowledge of archaeal and bacterial diversity and metabolic requirements. As a result, most of what we now know about rumen microbes comes from a small number of well-studied cultured lineages or reconstructed genomes from uncultured lineages. Even though this period of rapid genome-driven discovery has yielded numerous critical new insights into rumen microbial life, it is critical to isolate and culture species from these uncultured lineages to test genome-based predictions about their cell biology and physiology to comprehend their ecological roles fully.

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Table 1  Studies found in Web of Science with research terms “rumen” and isolates, spanning the period 1947-2022, reporting at least one new microbial isolate characterized phenotypically or phylogenetically.

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<th>Authors</th>
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<td>Bryant, MP; Doetsch, RN</td>
<td>A Study of Actively Cellulolytic Rod-Shaped Bacteria of the Bovine Rumen CHARACTERS OF ORGANISMS ISOLATED FROM THE RUMEN OF COWS FED HIGH AND LOW ROUGHAGE RATIONS</td>
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<td>Bauman, HE; Foster, EM</td>
<td>The characteristics of strains of selenomonas isolated from bovine rumen contents</td>
<td>J BACTERIOL</td>
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<td>The proteolytic system of a gram negative rod isolated from the bovine rumen Degradation and utilization of isolated hemicellulose BY pure cultures of cellulolytic rumen bacteria</td>
<td>J GEN MICROBIOL</td>
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<td>Hunt, WG; Moore, RO</td>
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**Notes:**
- DOI: Digital Object Identifier
- Page numbers are not provided directly, assuming standard page numbers for journal articles.