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Novel insights into the microbiology of fermented dairy foods

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Fermentation is a traditional approach to food preservation that, in addition to improving food safety, also confers enhanced organoleptic, nutritional, and health-promoting attributes upon those foods.Dairy products can be fermented by a diverse microbiota. The accompanying microbes can be studied using a variety of different, including 'omics'-based, approaches that can reveal their composition and functionality. These methods have increasingly been recently applied to study fermented dairy foods from the perspective of genetic diversity, functionality and succession. The insights provided by these studies are summarised in this review.

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Introduction

Fermented foods are generally defined as those foods or beverages made through controlled microbial growth and enzymatic conversions of major and minor food components [1••]. The fermentation of foods involves the breaking down of complex constituents into simpler ones, many of which can possess bioactive properties, through the use of microorganisms. Nutritional and functional properties are enhanced through the fermentation process. These include the improved availability of trace minerals, vitamins and anti-oxidants as well as greater safety, shelf-life and sensory attributes. Human cultures across the globe have been consuming fermented dairy products for millennia, exploiting the biochemical action of microorganisms naturally present in the raw milk, microorganisms that are in the surface of containers in which the dairy foods are placed or through a process known as back-slopping, whereby some of the material from a previous fermentation is employed to inoculate fresh substrate [2]. In the last century, and coinciding with the large scale, commercial production of fermented foods, came the use of starter and adjunct culture(s). More recently, the health benefits of many fermented dairy products have been the subject of intense investigation. Some examples include specific studies demonstrating the impact of kefir consumption on bone mineral density and bone metabolism [3], evidence of a reduced risk of type 2 diabetes associated with yogurt consumption [4,5] and investigations revealing that a fermented milk product containing a variety of microorganisms affects the activity of brain regions that control emotion and sensation [6]. These and other health-promoting features, combined with a view of fermented foods as 'natural' has further increased the popularity of fermented dairy foods [7] such as yogurts, fermented or cultured milks, kefir, acidophilus milk, koumiss, curd, buttermilk and cheeses. These are produced by the fermentation of different types of milk by specific microorganisms or complex microbial communities. This review will describe recent developments relating to the best known dairy fermented foods and the microorganisms that contribute to their fermentation.

Yogurt and cheeses

Protosymbiotic cultures of *Streptococcus salivarius* subsp. *thermophilus* (*Str. thermophilus*) and *Lactobacillus delbrueckii* subsp. *bulgaricus* (*Lb. bulgaricus*) are typically used to convert milk into yogurt. The strains involved have been exposed to a natural selection pressure imposed during yogurt production that, in the case of *Lb. bulgaricus*, contributed to the genetic evolution of ancestral strains with intermediate acetaldehyde-producing capabilities [8]. As was demonstrated in a recent study of lactic acid bacteria isolated from a range of traditional Greek dairy products, such products can also be a valuable source of novel strains with different health-promoting properties [9].

Cheese is the most popular fermented milk product. Both soft and hard cheeses are produced by culturing milk for a period of time. Certain types of cheeses can be made simply by straining the moisture out of sour cream or yogurt, while others require additional steps in the culturing and fermentation process. Large scale production of cheeses relies on the use of commercial starter culture (s), and the addition of adjunct cultures. Adjuncts can impart specific flavours [10] or may be probiotic candidates that are being delivered within the cheese [11•], thereby opening new opportunities for the design of dairy fermented foods for target populations. The combined probiotic properties of lactic acid and propionic acid bacteria were employed by Plé and colleagues who developed a pressed cheese containing *Propionibacterium freudenreichii* and *Lactobacillus delbrueckii* strains previously selected for their anti-inflammatory properties [12]. Studies of the microbiology of cheese have been revolutionised recently through in-depth functional genomic and metagenomic studies, which have demonstrated the microbial diversity of a vast variety of cheeses. These studies are of great value from an applied perspective and have further highlighted the fact that microbial communities are rich and diverse in cheeses and are critical to the typical organoleptic characteristics of traditional products [13,14]. Such analyses can also contribute to the selection of new strains as starter cultures for the dairy industry [15]. In addition, these investigations have also highlighted that cheese can provide valuable model systems for microbial ecology studies [16,17], including the shaping of microbial communities through horizontal gene transfer [18].

Fermented milks

Fermented milk is produced through the coagulation of milk, without the elimination of serum, by bacterial cultures that generally remain present until consumption. There are three categories of fermented milks: Thermophilic sour-milks (e.g. Matzoon), where the fermentation is conducted at 42–45 °C with lactic acid production; Mesophilic sour-milks (e.g. Cultured buttermilk, Viili, Ymer, Skyr), where the fermentation is conducted at 20–30 °C with lactic acid production; and acid and alcoholic milks (i.e. Kefir, Gioddu), where the fermentation is conducted at 15–25 °C with the production of some alcohol in addition to lactic acid and carbon dioxide (Table 1).

Many drinkable fermented milk products are produced by the addition of water to yoghurt or by the addition of cultures of *Str. thermophilus* and *Lb. bulgaricus* to standardized milk for fermentation at room temperature. However, efforts continue to commercialise other such fermented milks. Indeed the traditional Turkish fermented-milk drink, Ayran, and a spontaneously fermented yoghurt-like product made in Ghana and other parts of West Africa, Nunu, have recently been studied in order to improve quality and shelf-life stability to, ultimately, facilitate commercialisation [19,20•]. In the case of Ayran, in addition to *Str. thermophilus* and *Lb. bulgaricus*, this fermented milk contains *Lb. helveticus*, *Lb. fermentum* and *Lb. paracasei*. These additional cultures allow fast acidification and extensive proteolysis [21•]. Acidophilus milk is a traditional milk fermented with *Lb. acidophilus* in pasteurised-standardized milk [22]. The milk is inoculated and incubated at 37 °C for 18–20 h and, because of its strong acid taste, its consumption is more typically associated with a desire to address health-related issues, such as alleviating lactose maldigestion, than on the basis of flavour [23].

Specific milks (e.g. yak, cow and mares' milk) are used for the production of some fermented dairy drinks. This, together with environmental factors, starter and adjunct cultures and fermentation parameters (duration, temperature and storage vessel) shape the microbial diversity of naturally fermented milks [24••]. In the case of koumiss, mare's milk is fermented in containers made of animal skin or wooden casks. Fermentation occurs naturally at ambient temperature after the addition of filtered mare milk into a container containing old koumiss, which serves as the starter culture [25]. Shubat or Chal is a traditional fermented camel's milk that is generated through the action of *Lb. helveticus* and *Str. thermophilus*, resulting in a beverage with hypotensive effects [26]. Camel's milk is also used for the production of Gariss, a traditional Sudanese raw fermented dairy product [27].

Buttermilk was originally produced as a by-product of butter making and contains protein, phospholipids, fat, lactose, and minerals. *Lactococcus lactis* subsp. *cremoris* (*Lc. lactis* subsp. *cremoris*) or *Lc. lactis* subsp. *lactis* biovar. *diacetylactis* (*Lc. lactis diacetylactis*) (Table 1) are typically responsible for this fermentation and the production process includes a heat treatment of the milk to 95 °C followed by a cooling phase to 20–25 °C before the addition of the starter culture. Starter is added at 1–2% and the fermentation is allowed to proceed for 16–20 h [6]. The milk fat globule membranes (MFGMs) found in buttermilk is rich in unique bioactive proteins [28] and is the major protein-containing constituent of this fermented product. Other buttermilk-based fermentations are combined with plants and fruits, as in the case of Omashikwa, a Namibian artisanal product made from tree roots (*Boscia albitrunca*) added to the fermented buttermilk. This product is dominated by *Lb. fermentum* and *Kluyveromyces marxianus* [27].

Starter cultures, adjuncts and complex fermenting communities

In addition to producing acid for preservation purposes, starter cultures, which include a variety of bacteria, yeasts and moulds, allow for a more controlled and predictable fermentation in terms of sensory-related features, appearance and other physical and chemical characteristics. Starter cultures consist of one or more (referred to as a co-culture or mixed culture) fermenting species [29]. Undefined starter cultures also continue to be relevant in traditional dairy foods fermentation and consist of complex uncharacterized microbial community, which can be revealed with high-throughput DNA sequencing technologies and predictive metabolic modelling [30]. During the growth of dairy starter bacteria, which are typically Lactic Acid Bacteria (LAB), in milk, the initial metabolism of lactose results in the formation of glucose