Advantages and disadvantages of non-starter lactic acid bacteria from traditional fermented foods: potential use as starters or probiotics

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ABSTRACT

Traditional fermented foods are a significant source of starter (sLAB) and/or non-starter lactic acid (nsLAB) bacteria. Moreover, these microorganisms are also known for their role as probiotics. The potential of nsLAB is huge, however there are still challenges to overcome between characterization and application. In the present review, the most important steps that autochthonous lactic acid bacteria isolated from fermented foods need to overcome, to qualify as novel starter cultures, or as probiotics, in food technology and biotechnology, are considered. These different characterization steps include precise identification, detection of health-promoting properties, and safety evaluation. Each of these features is strain-specific and needs to be accurately determined. This review highlights the advantages and disadvantages of nsLAB, isolated from traditional fermented foods, discussing safety aspects and sensory impact.

Keywords: Non-starter lactic acid bacteria (nsLAB), probiotics, fermented foods, acidification activity

1. INTRODUCTION

Lactic acid bacteria (LAB) are food fermentation agents involved in the manufacturing of yogurt, cheese, cultured butter, sour cream, sausages, cucumber pickles, olives, sauerkraut, and cocoa, among many other foods (Nguyen et al., 2015; Todorov et al., 2017; Ho et al., 2018; Touret et al., 2018; Mannaa et al., 2019 and Kazou et al., 2021). However, some LAB species may spoil beer, wine, and processed meats (Ray & Joshi, 2015; Laranjo et al., 2017). According to their specific roles, LAB involved in fermentation processes, can be divided into two groups: starter lactic acid bacteria (sLAB) and non-starter LAB (nsLAB). sLAB may be added as starters and adjunct cultures. According to Medina-Pradas et al. (2017), a starter is a culture of living microorganisms, which are used to begin fermentation, producing specific changes in the chemical composition and sensory properties of the food product. On the other hand, nsLAB usually originate from the production and processing environments as spontaneous/ autochthonous microbiota. There is some diversity in nsLAB, depending for example, on cheese variety, processing, and duration of ripening (Blaya et al., 2018). Any culture whose primary role is not acid production, can be named nsLAB. These are bacteria that grow in fermented foods during ripening but are not deliberately added and are not required for acid production at the beginning of the manufacturing process (Leeuwendaal et al., 2021). nsLAB are used to balance some of the biodiversity removed by pasteurization, improve hygiene, and for natural food preservation. These cultures have a significant impact on flavour and accelerate the maturation process (Bintsis, 2018a). However, some nsLAB can act as sLAB, depending on the food matrix. One example is *Lactiplantibacillus plantarum* (formerly classified as *Lactobacillus plantarum*), which is used as a starter culture in meat and wine (malolactic) fermentation, while it can be considered as nsLAB in the dairy sector (Laranjo et al., 2017; Brizuela et al., 2018a).

In traditionally manufactured fermented foods, the population of nsLAB is often not monitored, so these products are a main reservoir of unexplored microbial communities, which can be a source of some new properties for application in the food industry (Todorov et al., 2017; Muruzović et al., 2018a).

There are diverse geographical areas in the world, which are known for their artisanal way of producing fermented foods. Traditional fermented foods are produced using different manufacturing techniques, raw materials, and microorganisms depending on the available raw materials and local practices (Motahari et al., 2017). Some examples of fermented foods include *kimchi* (Mannaa et al., 2019), *kombucha* (Nguyen et al., 2015), *sauerkraut* (Touret et al., 2018), *lukanka* (Todorov et al., 2017), *cocoa* (Ho et al., 2018), and *kefir* (Kazou et al., 2021), among others. Most of these fermentations are carried out without the addition of commercial starter cultures (Muruzović et al., 2018a; Žugić Petrović et al., 2019; 2020). Therefore, many authors emphasize the importance of artisanal products as valuable sources of nsLAB, with unique technological and putative probiotic features, important both as a base for scientific research, as well as for the designing novel starter cultures for functional foods (Settanni & Moschetti, 2010; Motahari et al., 2017; Hayaloglu, 2016; Muruzović et al., 2018b; 2018c).

Considering that many reports have highlighted the importance of nsLAB in traditional fermented foods, the aim of this review is to contribute to the understanding of the following questions: (i) what are the major hurdles regarding the characterization of non-starter LAB?; (ii) what are the most commonly nsLAB in fermented foods and how do they contribute to food preservation?; (iii) what is the contribution of nsLAB to specific organoleptic features?; (iv) what does it mean to have probiotic potential?; (v) how can these isolates be used as new starter cultures and/or as “probiotic enrichment“; and (vi) which is their role in the improvement of food quality?

Overall, the present review highlights the role of autochthonous non-starter lactic acid bacteria (nsLAB) as novel starters, or probiotics, in dairy and non-dairy fermented foods.

2. CHARACTERIZATION OF LACTIC ACID BACTERIA – IDENTIFICATION AND SAFETY ASSESSMENT

Identification of beneficial microbes relied for decades on phenotypic methodologies, which are often linked to the ambiguous, limited characterization of the organisms under study (Sharma et al., 2020). Those conditionings increased the interest on a reliable classification of relevant microorganisms and led to the development and optimization of a panoply of molecular tools. This review gathers information on the molecular identification methodologies usually applied for the identification and classification of bacteria with high significance on food science and related settings. A main obstacle continues to be the lack of consistent identification systems to be applied for all lactic acid bacteria, since distinct techniques may work for one of the genera but show limited application for others.

Although molecular-based techniques are comparatively superior to conventional microbiological procedures, each presents advantages and disadvantages, either related with discrimination power, repeatability/reproducibility, difficulties on the applicability, or results interpretation. Furthermore, the costs associated, or the time required for experimental performance and data analyses, must not be overlooked.

The present manuscript gathers information on the application of identification and differentiation methods, previously applied for the characterization of lactic acid bacteria. To facilitate overview, **Table 1** compiles a plethora of molecular tools and corresponding features.

Overall, criteria such as (i) discriminatory power, (ii) repeatability/reproducibility, (iii) data analysis/interpretation and (iv) associated cost, should be considered for the selection of the most adequate technique for each study. No single technique provides all the information on inter and intra-species differentiation. Therefore, a reliable identification and differentiation of lactic acid bacteria should follow a sequential polyphasic approach.

Furthermore, it is well known that genus and/or species allocation is often not enough to guarantee safety. Hence, the selection of microbes to be used in food, requires the access to international databases which list safe microorganisms. This concept, known as GRAS-Generally Recognized as Safe in USA or QPS-Qualified Presumption of Safety in Europe, is fundamental while working in food science.

In more detail, regarding Europe, a microorganism must meet the following criteria to be granted the QPS status: (i) its taxonomic identity must be well defined; (ii) the available body of knowledge must be sufficient to establish its safety; (iii) the lack of pathogenic properties must be established and substantiated and (iv) its intended use must be clearly described (EFSA, 2020). Thus, the selection of microrganisms to be used as starter cultures or probiotics, must involve the detailed analysis of the microorganism(s) of interest, regarding reliable identification (using methodologies as the ones described in **Table 1**) and safety assessment, i.e., screening for antimicrobial resistance (Fraqueza, 2015; Li et al. 2020; Daniali et al. 2020) and virulence factors (Semedo-Lemsaddek et al. 2012), both at phenotypic and genotype level. Currently, the advent of high-throughput-sequencing significantly reduced the costs associated with vanguard methodologies such as Whole Genome Sequencing (WGS), turning them affordable for numerous laboratories, but major disadvantages continue to be the large amount of complex data analysis and the low quality of the databases available for comparison.

WGS provides a comprehensive picture of all genome content, allowing the identification of virulence, antibioresistance or probiotic/technological-related determinants (Tyson et al., 2018; Mannaa et al., 2019; Nethery et al., 2019; Rodrigo-Torres et al., 2019; Dong et al. 2019; Waseem et al. 2017). The quick and reliable identification of microbes responsible for foodborne outbreaks (Gerner-Smidt et al., 2019), may lead to fast food recalls, contributing to prevent further health risks for the consumers. Moreover, genomic data can also be used to achieve a reliable selection of strains with technologic or probiotic potential.

Nevertheless, the major challenge continues to rely in deciphering bacterial potential from genetic information. The progress of multi-OMIC technologies and application of a systems biology approach (O'Donnell et al. 2020) may shed light on food-related microorganisms and help explore their full potentials.

3. USE OF NON-STARTER LAB AS STARTER CULTURES - ACIDIFICATION ACTIVITY

The major metabolic trait associated with LAB is the production of lactic acid from the fermentation of carbohydrates, which is known as food acidification or primary acidification process (Bintsis et al., 2018b). Acid production by LAB generates stressful conditions for pathogenic or spoilage microorganisms present in traditionally fermented foods, by reducing pH values, thus improving the hygienic properties and prolong safe storage of the final products (Papadimitriou et al., 2016). On the other hand, a pH of 5.1 to 5.3 has a positive effect on the moisture of the fermented foods since low pH induces a decrement in the water retention, therefore, the maturation processes are accelerated (Todorov et al., 2017).

Raw milk is known to be a major source of nsLAB. Most nsLAB are salt-and acid-tolerant, facultative anaerobes, and therefore grow quite well in cheese, and other dairy products, where they are responsible for the ripening process (Hayaloglu, 2016; Muruzović et al., 2018c). In raw milk cheeses made without the addition of starter cultures, nsLAB show a role in both acidification and coagulation, as well as in cheese maturation. In previous reports, Muruzović et al. (2018a; 2018b) and Grujović et al. (2019b) investigated the acidification and coagulation ability of nsLAB isolated from raw milk cheese, demonstrating their acidification ability, especially regarding lactobacilli and lactococci, which showed the ability of curdle formation in pure and enriched milk. These results suggest the potential of nsLABs to be used both as starter cultures and for ripening and flavour development.

In contrast to starters, the initial number of nsLAB in cheese is relatively low (approximately 100 CFU/g), but they grow rapidly to high numbers (around 10^8

CFU/g), within the first few days of ripening (Hayaloglu, 2016). Growth rate depends primarily on the strains present, ripening temperature, and moisture content of the cheese (Hayaloglu, 2016; Muruzović et al., 2018b). nsLAB mainly comprise heterofermentative lactobacilli, especially *Lacticaseibacillus casei* (formerly classified as *Lactobacillus casei*) and *Lacticaseibacillus paracasei* (formerly classified as *Lactobacillus paracasei*), as well as *Pediococcus* spp. and heterofermentative lactobacilli (*Levilactobacillus brevis* (formerly classified as *Lactobacillus brevis*) and *Limosilactobacillus fermentum* (formerly classified as *Lactobacillus fermentum*), which are occasionally found (Hayaloglu, 2016; Muruzović et al., 2018b).

Meat products, mostly dry-fermented sausages, are slowly cured through spontaneous fermentation by autochthonous (non-starter) microbiota, present in the raw materials or introduced during manufacturing (Semedo-Lemsaddek et al., 2016). nsLAB participate in the coagulation of muscle proteins by acidifying the batters, which results in increased slice stability, firmness, and cohesiveness of the final product. They also contribute to the flavour of the final product, through formation of noticeable acidic tastes. Furthermore, the existing acidic conditions may increase the activity of cathepsin D, which is responsible for muscle proteolysis (Laranjo et al., 2017). In traditionally manufactured meat products, enterococci and lactobacilli are the dominant nsLAB (Semedo-Lemsaddek et al., 2016; Correia Santos et al., 2017; Alfaia et al., 2018; Mrkonjic Fuka et al., 2020; Žugić Petrović et al., 2020).

Vegetables are also an important niche for the isolation and selection of nsLAB for starter and probiotic applications. Naturally and actively present nsLAB in many vegetable fermentations are *Leuconostoc mesenteroides*, *Pediococcus pentosaceus*, *Pediococcus acidilactici*, *Levilactobacillus brevis*, *Lactiplantibacillus plantarum*, and *Lactiplantibacillus pentosus* (formerly classified as *Lactobacillus pentosus*), but

Weissella spp. can also be present during the early stages of sauerkraut production (Medina-Pradas et al., 2017). Many authors indicated the acidification potential of nsLAB isolated from vegetables, such as fermented stink beans (sataw-dong) (Jampaphaeng et al., 2017). Sáez et al. (2018) indicated that nsLAB of dairy origin and nsLAB from olives and pickles, reached the lowest pH after 24 h and the highest acidifications rates. They suggest the potential use of nsLAB as starter cultures for obtaining standardized, high quality fermented vegetable.

In winemaking, malolactic fermentation (MLF) can be facilitated by autochthonous LAB or be induced by inoculating with selected bacterial starters, such as *Oenococcus oeni* and *Lactiplantibacillus plantarum*. However, in uninoculated MLF performed by autochthonous LAB, the conversion of malic acid into lactic acid can be slow or incomplete, or undesired volatile compounds and potentially hazardous compounds can be produced. Therefore, the use of bacterial starters can help minimize these risks (Virdis et al., 2021). Efforts have been directed to exploring the biodiversity of wine associated geographic areas, with the aim of finding new nsLAB which to be used as starters with a high degree of adaptation to each specific niche (Miranda-Castilleja et al., 2016; López-Seijas et al., 2020). For example, two potential new autochthonous MLF starters with interesting β-glucosidase activity, *Lacticaseibacillus paracasei* (formerly classified as *Lactobacillus paracasei*) UVI-2 and *Lentilactobacillus hilgardii* (formerly classified as *L. hilgardii*) UVI-23, have been identified from Albariño grapes in Val do Salnés, Spain (López-Seijas et al., 2020). This is especially interesting considering that the regional identity of wines can be an important factor in increasing the value of the final product (Bartowsky et al., 2015). In recent years, mixed inoculation strategies have also been attempted. The use of commercially available blended cultures of *L. plantarum* and *O. oeni* as MLF starters can facilitate a rapid consumption of malic acid, whilst contributing significantly to the volatile profile of wine (Brizuela et al., 2018b). Therefore, the use of non-starter LAB as starter cultures in winemaking showed a great potential and gives evidence for further research.

4. ROLE IN FOOD PRESERVATION - ANTIMICROBIAL POTENTIAL OF NON-STARTER LAB

Numerous studies have confirmed the antimicrobial potential of nsLAB isolated from fermented foods. In addition, Cheong et al. (2014) showed that LAB isolated from various herbs, fruits, and vegetables possess antifungal and antimycotoxigenic activity. Fraga Cotelo et al. (2013) indicated the antimicrobial activity of nsLAB isolated from cheese against pathogens like *Escherichia coli*, *Staphylococcus aureus*, or *Listeria monocytogenes*. Several lactobacilli, which include *L. plantarum*, *L. fermentum*, *Lactobacillus sakei* and *L. curvatus*, have been reported as bacteriocin producers and have been used as protective cultures in dairy and meat products (Heredia-Castro et al., 2015; Cecilia Fontana et al., 2015; Casaburi et al., 2016; Muruzović et al., 2018a; 2018b; Fraqueza et al., 2021). Moreover, *Lactococcus* spp. and *Enterococcus* spp., isolated from raw milk, traditional cheeses, meat products, and some fermented vegetables showed inhibitory activity against many Gram-positive and Gram-negative species (Pisano et al., 2015; Henning et al., 2015; Medina-Pradas et al., 2017; Muruzović et al., 2018a; 2018b; Grujović et al., 2019b).

Lactic acid and natural antimicrobial peptides, known as bacteriocins and bacteriolysins produced by LAB, can be used to improve the quality and safety of fermented foods, by inhibiting the growth of pathogens (Scatassa et al., 2017; Laranjo et al., 2017). Bacteriocins are antimicrobial peptides or proteins, that may suffer posttranslational modifications, with the ability to outcompete other bacterial species (Alvarez-Sieiro et al., 2016). Bacteriocin classification and description, including mechanism of action, is given in **Table 2**. Besides bacteriocins, a new class of antimicrobial peptides, bacteriolysins, have been described as hydrolytic polypeptides (Güllüce et al., 2013). Glycocin F is the most studied bacteriolysin, it is produced by *Lactiplantibacillus plantarum* and has bactericidal activity against a wide range of Gram-positive bacteria (Amso et al., 2018).

Although results obtained from *in vitro* assays have shown that several bacteriocins inhibit target organisms, their application must be tested, to confirm *in situ* effectiveness. Many studies showed the putative application of bacteriocins or bacteriocin-producing nsLAB strains into foods, such as meat products, dairies, and fish, but only a few of them have been commercialized as food preservatives. These data were reviewed in detail by Settanni & Moschetti (2010). It is crucial to emphasise that screening for bacteriocins to be applied in food products, requires the fulfilment of some important criteria (Silva et al., 2018): Producing strains should be food grade, exhibit a broad spectrum of inhibition, harbour high specificity, have no associated health risks, present beneficial effects (e.g., improve safety, quality, and flavour of foods), display heat and pH stability, and optimal solubility and stability for a particular food (Silva et al., 2018). A list of commercially available bacteriocins is shown in **Table 3**.

5. POTENTIAL USE OF NON-STARTER LAB AS PROBIOTICS

According to Hill et al. (2014), probiotics have been defined as live microorganisms that, when administered in adequate amounts, confer a health benefit on the host. They are usually considered dietary supplements, and contain viable non-pathogenic microorganisms, that interact with the gastrointestinal microbiota or directly with the immune system (Kook et al., 2019). Probiotics are normally included in food products, known as functional foods. Lactic acid bacteria are the microorganisms most commonly used as probiotics (Shokryazdan et al., 2014). However, even though most LAB have a GRAS status, it is well known that some LAB (including *L. rhamnosus* GG) may act as infectious microorganisms, particularly in immunocompromised individuals (Kochan et al., 2011). On the other hand, other microorganisms, such as yeast *Saccharomyces cerevisiae* and some *Escherichia coli* and *Bacillus* sp. strains, can also be used as probiotics (Song et al., 2012).

Furthermore, the dual role of enterococci in food technology, as bacteriocin producers or potentially hazardous food contaminants, is well known. Their limited use as probiotics is due to their antimicrobial resistances (especially vancomycin-resistance) and horizontal gene transfer events. Enterococci can easily incorporate several genes, such as antimicrobial resistance determinants or virulence factors, which can be considered hazardous (Suvorov, 2020; Grujović et al., 2021). However, these bacteria are commonly used in the food industry for preservation, because they are natural lactate producers and can produce bacteriocins. In addition, they can survive in different compartments of the intestinal system and normally inhabit the human gut (Suvorov, 2020). Nevertheless, enterococcal strains have been used as probiotics in Europe. Successful commercial examples coming from different countries include Linex (LEK, Slovenia), Symbioflor 1 (Symbiopharm, Germany), and

Laminolakt (Avena, Russia) (Suvorov, 2020). *Enterococcus faecalis* strain (Symbioflor®, Symbiopharm, Herborn, Germany) has been sold as a pharmaceutical probiotic for more than 50 years, without any report or documentation of infections or adverse effects (Fritzenwanker et al., 2013; Baccouri et al., 2019). Therefore, generally recognized safety guidelines for probiotics need to be carefully established. Furthermore, a case-by-case assessment is mandatory for each enterococcal isolate, since there is no universal strain that would provide all probiotic benefits, as highlighted by Solieri et al. (2014).

For probiotics to be successful, a strain should be able to show health-promoting metabolic activity and colonize the gastrointestinal tract, although the latter is not crucial for delivering beneficial effects. The safety and functional properties of strains, such as antimicrobial resistance and adherence to the intestinal mucosa cells, as well as the possibility of immunomodulation, are very important for the selection of potential probiotics and should be studied using reliable *in vitro* screening methods (Kook et al., 2019).

Safety evaluation

As aforementioned, investigation regarding safety aspects must include an evaluation on the ability of nsLAB to synthesize extracellular protein toxins, and resistance to antimicrobials, both at the phenotypic and genotypic level.

The most usual protein toxins identified in LABs are of the Hemolysin protein family which cause damage to various cellular elements, especially the lysis of erythrocytes and the release of haemoglobin. Hemolysin and Hemolysin-III are commonly found in many close organisms, such as *L. casei*, *L. paracasei*, *L.*

rhamnosus, *Lacticaseibacillus zeae* (formerly classified as *Lactobacillus zeae*) and *Lacticaseibacillus saniviri* (formerly classified as *Lactobacillus saniviri*) (Surachat et al., 2017). Lactobacilli can grow normally without iron, which is an ecological advantage in the natural environment, where they compete with pathogenic bacteria. That advantage could imply that the Hemolysin protein family found in lactobacilli does not cause the lysis of human erythrocytes, which has been confirmed by different studies (Songisepp et al., 2012; Surachat et al., 2017; Grujović et al., 2019a). Nevertheless, haemolysis assays using blood agar plates are a criterion related to the safety aspect of the potential probiotic strain that cannot be overlooked (Yasmin et al., 2020).

The European Food Safety Authority (EFSA) has established the updated guidance document on the assessment of antimicrobial resistance in LAB (EFSA, 2018). Determination of antimicrobial resistance profiles is based on: i) phenotypic testing and determination of minimum inhibitory concentrations (MIC) and ii) whole genome sequencing (WGS), with the analysis of both chromosomal and extrachromosomal genetic elements for the detection of known antimicrobial resistance (AMR) determinants. Bacterial strains carrying mobile genetic elements (MGE) harbouring antimicrobial resistances should not be used in food, feed, or as probiotics (EFSA, 2018). In fact, it is well documented that AMR is often associated with MGEs, which promote their mobility, enabling a rapid spread throughout the bacterial community (Fraqueza, 2015). Tóth et al. (2021) also indicated that numerous AMR determinants are associated with integrated MGEs (transposons, integrons, or insertion elements), conjugative plasmids or phages, thus promoting horizontal gene transfer (HGT). The intrinsic antimicrobial resistance, caused by non-transferable resistance genes, does not raise such concern, as it exhibits a low risk of AMR genes' dissemination, opposite to the acquired resistance caused by determinants located on MGEs (EFSA, 2018).

Previous reports have described LAB antimicrobial resistance profiles in detail (Vesković Moračanin et al., 2017; Thumu & Halami, 2019; Dušková et al., 2020; Das et al., 2020, Ojha et al., 2021; Flórez et al., 2016; Zarzecka et al., 2020; 2022; Jaimee & Halami, 2016; Anisimova & Yarullina, 2020; Yasir et al., 2020; Guo et al., 2017). There is a wide data collection reporting intrinsic resistances towards different classes of antimicrobials, namely beta-lactams, tetracyclines, macrolides, quinolones, aminoglycosides, and glycopeptides (Vesković Moračanin et al., 2017). Regarding acquired AMR determinants, some of the most frequently identified correspond to tetracycline (encoded mainly by *tetM*, *tetS*, *tetW*, *tetK*, *tetO*), macrolides (encoded by the *ermA*, *ermB* and *ermC*) and chloramphenicol (encoded by cat) (Dušková et al., 2020; Das et al., 2020, Ojha et al., 2021). Moreover, Anisimova & Yarullina (2020) have indicated that resistance to erythromycin, tetracycline and chloramphenicol should be the most closely monitored, due to the frequent association with specific MGEs, namely with the Tn916-Tn1545/Tn917 transposon family, which are responsible for the widespread occurrence of those traits (Thumu & Halami, 2019).

The food chain can be considered a main disseminator of antimicrobial resistant bacteria or determinants, allowing the spread of AMR from food-related microorganisms to potentially pathogenic bacteria, or other commensals present in the gut microbiota (Ojha et al., 2021). Therefore, it is essential to perform a careful case-by-case evaluation. In fact, previous studies have indicated that AMR genes detected in food-LAB can be transferred to commensal bacteria or pathogenic bacteria through HGT, which may pose a serious threat to food safety and public health. The most frequently occurring transfer is that of tetracycline and macrolide resistance determinants (Flórez et al., 2016; Thumu & Halami, 2019; Ojha et al., 2021, Zarzecka et al., 2020; 2022), but the transference of other resistance genes (aminoglycosides, quinolones) has also been reported (Jaimee & Halami, 2016; Anisimova & Yarullina, 2020). In a recent study by Yasir et al. (2020), a total of 36 ARGs and the transposase, integrase, and recombinase genes were detected in LAB isolated from pasteurized and unpasteurized Arabian laban. In addition, some authors point to the possibility of HGT from starter cultures microorganisms to pathogens present in food, especially during fermentation (Thumu & Halami, 2019). On the other side, some authors have indicated the non-transferability of AMR genes during *in vitro* or *in food* models (Flórez et al., 2016; Guo et al., 2017) suggesting, once again, the strain-dependent nature of the event.

Moreover, some lactic acid bacteria are also known for their ability to exhibit decarboxylase activity, which may lead to the production of biogenic amines from available amino acids (Alfaia et al., 2018; Özogul & Hamed, 2017).

Therefore, the complex safety evaluation of LAB requires a wide multidisciplinary approach, to predict and avoid undesirable public health consequences, along the entire food-production and distribution chain. Whole genome sequencing or a multi-OMICs approach may be relevant tools for this assessment.

nsLAB in synbiotics

One of the major interests in using nsLAB as probiotics is driven by the fact that upon consumption, these microorganisms can be beneficial to the host by boosting the good microbiota of the gastrointestinal tract (GIT) (Leeuwendaal et al., 2021). Moreover, since many health-promoting microorganisms belong to LAB, it makes sense to use traditional fermented foods as their main source. In fact, fermented foods are well suited to promote health associated with probiotic bacteria, considering that fermented cereals and dairy products already project a positive health image. Consumers are familiar with the fact that fermented foods contain microorganisms. Moreover, probiotics used as starter cultures can combine the positive images of fermentation and probiotic traits (Mokoena et al., 2016). However, although consumption of probiotics usually has a beneficial effect on consumers, we must not overlook the fact that a constant introduction of prebiotics and probiotics may increase certain genera of gut microbiota, leading to decreased microbial diversity. Therefore, as suggested by Khan et al. (2020), research should focus on understanding the mechanistic interactions between prebiotics/probiotics and gut microbiota.

Research on probiotics suggests a range of potential health benefits to the host organism (Song et al., 2012; Moreno et al.,2018); either humans, animals, or plants (Song et al., 2012). The *International Dairy Federation* recommended that probiotic dairy foods should contain at least 10^6 to 10^7 CFU/mL of probiotics at the time of consumption, to guarantee corresponding beneficial effects (Halim et al., 2017). Probiotic non-dairy foods are recommended to contain between 10^4 and 10^{10} CFU/mL or CFU/g of probiotics, depending on the type of product (Ranadheera et al., 2017). The viability of the microorganisms throughout processing and storage plays an important role in transferring the claimed health properties. The effect of probiotics on human health depends on the strain, dose, and components used to produce a given probiotic product. Nevertheless, although there are many positive effects on human health, some researchers have indicated that probiotics can impair human health. For example, probiotic microorganisms may cause systemic infections, disturb the metabolism, or participate in the horizontal gene transfer of antimicrobial resistance or virulence genes. Although probiotic bacteria usually have a beneficial effect on the digestive system, in the case of overdosing or usage by immunocompromised individuals, infections may overcome. Hence, considering the existence of reports on the adverse effects of probiotics, it is necessary to fully explore and understand their mechanisms of action and interaction with the host's microbiota (Markowiak & Śliżewska, 2017).

Food products that simultaneously contain probiotics and prebiotics, are known as synbiotics. Prebiotics have recently been defined as substrates that are selectively used by the host microbiota with beneficial health effects (Gibson et al., 2017). This combination ensures the survival of probiotics through the gut and facilitates delivery into the large intestine. Prebiotics also stimulate the growth and activity of probiotics in the intestinal microbiota. Most traditional fermented foods, such as cereal-based fermented porridges, beverages, fermented fruits, and vegetables (including roots or tubers), fermented milk products, and fermented meat products, fit the synbiotics definition perfectly, as they comprise residual stomach-indigestible polysaccharides, together with LAB responsible for both fermentation and health benefits. Hence, the use of natural probiotics offers an innovative approach for developing formulations applied as functional foods, aiming the management of chronic inflammatory gastrointestinal disorders and many other lifestyle diseases (Mokoena et al., 2016). Nevertheless, the major problem with the application of nsLAB as probiotics in food matrixes is the reduced growth and biomass concentration, owing to product inhibition, further emphasizing the need for *in food* models (Aguirre-Ezkauriatza et al., 2010).

Moreover, the use of nsLAB as probiotics together with prebiotics, such as inulin, has been shown to have an impact on sensory analysis. In fact, inulin is often used as prebiotic, also for its well-known role affecting taste, texture, and moisture in many foods (Illippangama et al., 2022). Some studies have reported the possibility of obtaining similar, or even better, performance with probiotic products, in comparison to conventional products, such as functional yogurt with *Limosilactobacillus reuteri* RC-14 (formerly classified as *Lactobacillus reuteri* RC-14), *L. rhamnosus* GR-1 and 0.4% of inulin (Hekmat & Reid, 2006), chocolate mousse with added inulin and *L. paracasei* (Aragon-Alegro et al., 2007), curdled milk with inulin, and *L. acidophilus* (Rodrigues et al., 2011), and milk fermented with *B. animalis* and *L. acidophilus* La-5, and supplemented with inulin (Oliveira & Jurkiewicz, 2009). In the production of fruit yogurt, sucrose, or some other sweeteners, are often added to milk. It is important to assure that the amount of sugar does not exceed 10% since this affects consumers' acceptance (Chollet et al., 2013; McCain et al., 2018). It is well-known that the addition of sugar to yogurt decreases the sour taste, which is due to the production of acids and acetaldehyde in yogurt by bacteria. However, high sugar content has a limited effect on water availability for proper microbial growth. Moreover, the relatively high acidity, the high concentration of organic acids, and the presence of hydrogen peroxide (at low concentrations) lead to a significant decrease in aroma and taste, as well as consumer's acceptance (Routray & Mishra, 2011; Chollet et al., 2013). Hoppert et al. (2013) reported that many consumers rated the regular-sugar yogurt as being too sweet and low in flavour. Cruz et al. (2013) also proved that the addition of prebiotics has a negative influence on the rheological properties of yogurt, leading to consumer's rejection.

Yogurt production depends on the synergism between *S. thermophilus* and *L. delbrueckii* subsp. *bulgaricus.* As aforementioned, probiotic bacteria can be added to the yogurt. However, before this kind of probiotic fermented product is manufactured, the interaction between starter cultures and added probiotic culture(s) needs to be fully investigated, in order to detect possible antagonistic effects (Jørgensen et al., 2019). Therefore, the selection, processing, and inoculation with nsLAB must be well considered.

Health benefits

Health benefits attributable to nsLAB involved in the production of functional food as probiotic cultures are numerous. Strains able to survive acid stress and bile tolerance usually show the ability to deconjugate bile via bile salt hydrolase (BSH) enzymes, which have also been linked to reduced serum cholesterol levels in the host organism (Leeuwendaal et al., 2021). Furthermore, bacterial adhesion ability can prevent immediate elimination by intestinal peristalsis and provides a competitive advantage in this ecosystem. However, many authors indicated that there was no correlation between hydrophobicity, auto-aggregation, and co-aggregation ability between potential probiotic strains. Previous studies indicated that auto-aggregation of probiotics is strain-specific (Ramos et al. 2013; Jampaphaeng et al. 2017). According to Han et al. (2017), several factors may influence the aggregative ability of probiotics, including cell surface charge, cell surface components, the size of the bacterial cell, and environmental conditions. Leeuwendaal et al. (2021) pointed out that probiotic nsLAB, in addition to the ability to colonize the human intestine, can also increase the concentration of secreted antimicrobial substances in the process of coaggregation, turning the control of pathogens much more efficient. Indeed, the presence of probiotic nsLAB in fermented food also contributes to normal functioning of the GI tract (Leeuwendaal et al., 2021), anti-viricidal activity (Garneau & Moineau, 2011; Whaling et al., 2012), antitumor properties (Aragón et al., 2014) and many other health benefits (Mokoena et al., 2016).

The positive health effects of probiotic nsLAB are achieved by specific metabolic traits, including bioactive peptide production (bacteriocins, hormones, enzymes, peptides with angiotensin-converting enzyme (ACE)-inhibitory activity, etc.) and γ-aminobutyric acid (GABA), as a non-protein amino acid (Settanni & Moschetti, 2010). For example, Ong et al. (2007) studied the ACE-inhibitory activity of *L. casei* strains, previously selected as probiotics, in Cheddar cheese. The authors found out that the IC_{50} (concentrations of ACE needed to inhibit 50% of ACE activity) of 24-week ripened cheese obtained with non-starter *L. casei* inoculation was lower than IC_{50} of 36-week ripened cheese processed without adjunct cultures. Cho et al. (2007) indicated that *Lb. buchneri* MS, isolated from kimchi, showed the ability to produce GABA in MRS broth with monosodium glutamate. The culture extract of *Lb. buchneri* MS partially or completely protected neuronal cells against neurotoxicant-induced cell death, showing its high potential in human health.

In addition, some bacteria, including specific nsLAB strains, are also capable of producing exopolysaccharides (EPS), high molecular-weight polymers produced from sugars, which can affect the host by modulating immune responses (Ryan et al., 2015). EPS also show antioxidant, anti-cancer and anti-ulcer activities (Abid et al., 2018), can be used to inhibit pathogens growth or as anti-biofilm agents (Patten & Laws, 2015). EPS also shows beneficial impact on blood glucose (Oleksy & Klewicka, 2018) and cholesterol levels (Korcz et al., 2018), as well as antihypertensive activity (Harutoshi, 2013).

6. ENZYMATIC ACTIVITY AND THE ROLE OF ENZYMES IN FOOD AROMA, FLAVOUR AND TASTE

Lactic acid bacteria exhibit a set of enzymatic activities that have a role in the development of aroma, flavour, and taste of fermented foods. nsLAB, which are naturally present in several foods, contribute to the fermentation processes and can eventually be added as starter cultures to enhance colour, reduce ripening time, and improve sensory characteristics, including flavour and aroma (García-Cano et al., 2019). In fact, LAB represent the majority of modern starter cultures (Laranjo et al., 2017).

Flavour can be defined as a combination of aroma and taste induced by a compound and perceived in the mouth. Flavour results from the perception of the taste compounds, associated to the five basic tastes (sweet, salty, bitter, sour, and umami), and the aroma volatile compounds. Together, they are responsible for the diversity of flavours that may be found in fermented foods (Thierry et al., 2015).

Aroma development is a two-step process, which includes the formation of precursor molecules, followed by the conversion of these into the actual aroma compounds.

Different food metabolites associated to taste arise in LAB fermented foods and are responsible for four of the five basic tastes or sensory qualities, namely sweetness and umami (aminoacids), bitterness (oligopeptides), and sourness (simple organic acids).

Three main enzymatic pathways have been identified in the metabolism of lactic acid bacteria, leading to the generation of flavour, namely the conversions of sugars (glycolysis), proteins (proteolysis), and lipids (lipolysis) (**Figure 1**).

Amylases, glycosidases, and other polysaccharide-degrading enzymes are responsible for the breakdown of sugars. Regarding proteolysis, different proteases and peptidases intervene. Moreover, glutamate dehydrogenase, aminotransferases, and ketoacid decarboxylase are some of the key lactic acid bacteria enzymes for flavour formation (Yvon, 2006). Glutamate dehydrogenase and aminotransferases are two main types of enzymes involved in the initial steps of amino acid catabolism, which plays a key role in the development of flavour. Ketoacid decarboxylase is a key enzyme in the Ehrlich pathway, concerting branched-chain amino acids to branched-chain acids or alcohols. Regarding the catabolism of lipids, esterases are lipases that hydrolase esters into an acid and an alcohol.

Different food products are fermented through the action of LAB, more specifically due to the activities of their enzymes, namely cheese and other dairy foods, kefir (Leite et al., 2015); and meat products (Laranjo et al., 2019).

Several classes of chemical compounds are accountable for food aroma, namely alcohols, aldehydes, ketones, fatty acids, esters, and sulphur compounds, among others (Smid & Kleerebezem, 2014). Some examples of fermented foods, LAB, aroma compounds and processes by which they are formed, are shown in **Table 4**.

LAB fermented foods harbor distinctive characteristic flavours, that can be attributed to different aroma and taste compounds, mainly volatiles, specific for each kind of fermented food, depending on the raw materials, as well as on their autochthonous and added starter microbiota.

7. OPTIMIZATION OF PROCESSING CONDITIONS FOR USAGE OF nsLAB AS STARTER CULTURES AND/OR AS PROBIOTIC AND CORRESPONDING ROLE IN THE IMPROVEMENT OF PRODUCT’S QUALITY

Fermentation confers certain advantages to foods: (i) food preservation due to the changes in pH and the presence of antimicrobials, such as organic acids, ethanol, and bacteriocins; (ii) changes in taste and texture, enriching organoleptic properties; (iii) specific benefits depending on the food matrix and type of fermentation, such as increasing the bioavailability of nutrients or removal of undesirable compounds, like toxic components and antinutrients.

In traditionally manufactured products, fermentation is done without the addition of commercial bacterial or fungal starter cultures. In most cases, fermentation is performed recurring to enzymes originated from fungi (Muruzović et al., 2018a; Vitorino et al., 2017) or with naturally present bacterial cultures (Medina-Pradas et al., 2017; Nkhata et al., 2018). Therefore, traditional food products are a source of nsLAB, which can potentially be used as starter cultures and/or as putative autochthonous probiotics. However, processing conditions, from the raw milk or meat to final dairy or meat products, as well as the production of fermented vegetables, constitute a challenge those bacteria need to overcome, in order to survive and achieve optimal growth and development. Those conditions include pH values, water activity, salt concentration, temperature, and food matrix composition.

Starter and non-starter lactic acid bacteria, both commercial and autochthonous, are fundamental in traditional foods, due to rapid acidification of the raw materials through the production of organic acids, primarily lactic acid, and other important by-products, such as acetic acid, ethanol, aroma compounds, bacteriocins, exopolysaccharides, and several enzymes. These by-products effectively enhance the products' shelf life, ensure microbial safety, improve texture, and ultimately contribute to the pleasant sensory profile of the product.

Milk, as a substrate for fermentation, is subjected to various treatments during manufacturing. One of the most important regarding the development and growth of nsLAB is optimal temperature (i.e., heat treatments), which will result in significant denaturation of whey proteins. Denatured whey proteins and casein are incorporated into the cheese curd and have a significant effect on cheese yield and composition, as well as in the development of nsLAB (Vitorino et al., 2017).

Moreover, the buffering capacity of milk products is also an important physicochemical characteristic that corresponds to the ability of the product to be acidified or alkalinised, which depends on several compositional factors, including small constituents (inorganic phosphate, citrate, organic acids) and milk proteins (casein and whey proteins). As the pH of cheese is reduced by lactic acid fermentation, both the buffer capacity and dry matter content increase (Salaün et al., 2005). The initial number and extension of the logarithmic phase of nsLAB, as well as the amount of nutrients, moisture content, and salt concentration are the most important factors for optimal development of nsLAB in dairy products (Vitorino et al., 2017).

Vitamin content in fermented milk depends on the autochthonous microbiota. Most vitamin B groups, especially riboflavin, thiamine, and nicotinamide, are two-fold increased, whereas vitamins B1, B2, and ascorbic acid decrease, via utilization by LAB present in milk (Yoshii et al., 2019; Sharma et al., 2020).

LAB-induced fermentation and acidification are known to increase the bioavailability of minerals in fermented milk, especially calcium, potassium, zinc, magnesium, potassium iodide, and phosphorus (Garcia-Burgos et al., 2020; Sharma et al., 2020).

As aforementioned, processing conditions by which the traditionally food is manufactured, are important for the activity of nsLAB or probiotics. For example, fermentation temperature crucially affects the characteristics of the final product. Probiotics have their optimum growth conditions around 37°C, the usual normal human body temperature. Since fermentations during yogurt production usually occur at approximately 43°C, the application of lower temperatures associated with prolonged fermentation times, can contribute to higher probiotic concentrations in the final product (Lengkey & Balia, 2014).

Water activity (a_w), the duration of fermentation and temperature, have effects on the growth of nsLAB and on the pH of meat products. Sausage incubation at optimum temperature, with facultative anaerobic conditions, causes rapid LAB growth, conversion of simple sugars into lactic acid and pH reduction. A post-mortem range of 4.5–7 µmol/g is not sufficient to lower down the pH; thus, simple sugars are added as substrate for LAB, bringing pH values to 4.6–5. For example, Mastanjevic et al. (2017) used 0.62 g glucose/kg of meat to reduce the pH by 0.1. Lactobacilli, as well as genera *Streptococcus, Pediococcus, Leuconostoc, Lactococcus,* and *Enterococcus*, perform three simultaneous functions in fermented sausages, they produce nitric oxide by reducing nitrate and nitrite, are responsible for the cured colour when combined with myoglobin, and lead to pH reduction by producing DL-lactic acid from glucose through anaerobic glycolysis (Bintsis et al., 2018b).

In many industries, vegetable fermentation still occurs spontaneously. Thus, the process is not fully predictable and sometimes can lead to spoilage. However, traditional vegetable fermentation is in line with the demand for natural, healthier foods. The production of acid and pH decrease, together with the presence of salt, are the essence of the production of stable and safe fermented vegetables. *Enterobacteriaceae*, aerobic spore-formers, LAB, and other groups of bacteria and yeasts may be active for several days, or weeks, depending on factors such as temperature, dissolved oxygen, salt (mainly sodium chloride) and carbohydrates concentration used in the cover brines. The main carbohydrates used during the fermentation of vegetables are fructose and glucose (about 1 - 5%) and malic acid, depending on the type of vegetables used (Medina-Pradas et al., 2017).

Mbye et al. (2020) indicated that microorganisms can survive under extreme environmental conditions. They pointed out that a comprehensive knowledge of the molecular machinery, which facilitates such environmental stress adaptation, would enable the usage of natural LAB as starter cultures and probiotics. Thus, proteomic studies of probiotics under different processing conditions can provide clues regarding the molecular basis of this stress adaptation. For example, heat shock proteins (HSPs), may improve probiotic heat tolerance during food processing, and increase the survival rate during freeze-drying. Both starter or non-starter LAB could activate cold tolerance genes that induce cold-shock proteins (CSP) and antifreeze protein expression, thereby enhancing cryotolerance. The expression of *hsp* genes by LAB is known to be stimulated by stresses occurring during food processing. Some strains can use the arginine deiminase pathway and glutamate (GABA system) as an energy source, as well as to overcome acid stress. These protein markers have been exploited for biotechnological applications, since they can help on the selection of robust strains, able to survive under such harsh conditions.

Overall, the use of nsLAB, as both starter cultures and probiotics, has several advantages over spontaneous fermentation: better control of the fermentation itself, reduction of ripening time, reduced growth possibility for pathogenic microorganisms, and improved quality preservation between batches (Laranjo et al., 2017). However, selecting adequate microorganisms for the development of functional fermented foods is a challenging task, due to the complexity of each step and the numerous assays required (Munekata et al., 2020). Selection screening involves (i) evaluation of probiotic potential, in this stage, the influence of digestion stressors (body temperature, pH, gastric juice, and bile salt resistance), intestinal colonization (auto- and co-aggregation, antimicrobial activity, and adherence to enterocytes), and safety aspects (susceptibility to antimicrobials, biogenic amine production and virulence factors) are decisive to define the probiotic viability of an isolate; (ii) species and strain identification of potential candidates using reliable methods and (iii) selection of starter candidates through the evaluating of indicators, like fast and persistent colonization of fermentation raw materials, production of organic acids (especially lactic acid), inhibition of competitive microbiota (both spoilage and pathogenic microorganisms), prevailing at reduced water activity ($a_w < 0.90$), and also preserving or enhancing the sensory attributes of the fermented food.

8. CONCLUSIONS

Non-starter LAB have often been neglected, since no recent studies have addressed them as a group, and they are usually seen only as the cheese bacteria interacting with starters. The current review has focused on nsLAB as a group and discussed their potential role in traditional dairy and non-dairy fermentations.

Traditionally fermented foods are natural sources of non-starter LAB. These autochthonous bacteria have a multifunctional role in food fermentations, associated mainly with safety and desirable metabolic features, such as acid production and bacteriocins. Because of such traits, nsLAB contribute to improve the product's shelf-life, to establish specific/characteristic organoleptic features, as well as to the microbial enrichment on putative probiotics. Hence, fermentation achieved with nsLAB leads to the improvement of texture, taste, and nutritional value of the final product.

In this review, nsLAB have been comprehensively characterised and tackled for their potential as probiotics and in the development of organoleptic features, regarding dairy and non-dairy fermented foods. Several investigations have shown the health benefits of probiotics associated with the consumption of milk or other dairies. However, health and sensory impact of probiotic bacteria in non-dairy foods is challenging and further research in this aspect is still needed. This review highlights the pros and cons of nsLAB as novel starters or probiotics, discussing safety aspects and sensory impact.

Nowadays, consumer's demand for safe, high-quality functional foods is increasing. Progress on molecular biology, physiology, and biochemistry of nsLAB enhances the possibility of producing safer high-value nutritive products, with health-promoting properties, which makes the research on the topic of Food Quality and Safety both challenging and demanding.

The potential of nsLAB is huge, however there are still challenges to overcome between characterization and application. The different steps in their characterisation include precise identification, detection of health-promoting properties, and safety evaluation. Each of these features is strain-specific and needs to be accurately determined. The challenge however is to confirm the effective health claims of each potential probiotic strain.

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Authors' contributions

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Conflicts of Interest

The authors declare that they have no conflicts of interest with the current work or its publication.

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REFERENCES

Abid, Y., Casillo, A., Gharsallah, H., Joulak, I., Lanzetta, R., Corsaro, M. M., Attila, H., & Azabou, S. (2018). Production and structural characterization of exopolysaccharides from newly isolated probiotic lactic acid bacteria. *International Journal of Biological Macromolecules*, *108*, 719–728. https://doi.org/10.1016/j.ijbiomac.2017.10.155

Abriouel, H., Franz, C. M. A. P., Omar, B. N., & Gálvez, A. (2011). Diversity and applications of *Bacillus* bacteriocins. *FEMS Microbiology Reviews*, *35*, 201–232. https://doi.org/10.1111/j.1574-6976.2010.00244.x

Aguirre-Ezkauriatza, E. J., Aguilar-Yáñez, J. M., Ramírez-Medrano, A., & Alvarez, M. M. (2010). Production of probiotic biomass (*Lactobacillus casei*) in goat milk whey: comparison of batch, continuous and fed-batch cultures. *Bioresource Technology, 101*, 2837–2844. https://doi.org/10.1016/j.biortech.2009.10.047

Alfaia, C. M., Gouveia, I. M., Fernandes, M. H., Fernandes, M. J., Semedo-Lemsaddek, T., Barreto, A. S., & Fraqueza, M. J. (2018). Assessment of coagulase-negative staphylococci and lactic acid bacteria isolated from Portuguese dry fermented sausages as potential starters based on their biogenic amine profile. *Journal of Food Science*, *83*(10), 2544-2549. https://doi.org/10.1111/1750-3841.14298

Alvarez-Sieiro, P., Montalbán-López, M., Mu, D., & Kuipers, O. P. (2016). Bacteriocins of lactic acid bacteria: extending the family. *Applied Microbiology and Biotechnology*, *100*, 2939–2951. https://doi.org/10.1007/s00253-016-7343-9

Amso, Z., Bisset, S. W., Yang, S. H., Harris, P. W. R., Wright, T. H., Navo, C. D., Patchett, M. L., Norris, G. E., & Brimble, M. A. (2018). Total chemical synthesis of glycocin F and analogues: S-glycosylation confers improved antimicrobial activity. *Chemical Science*, *9*(6), 1686-1691. https://doi.org/10.1039/c7sc04383j

Anisimova, E. A., & Yarullina, D. R. (2020). Antibiotic resistance and the mobility of its genetic determinants in *Lactobacillus fermentum*. *Molecular Genetics, Microbiology and Virology, 35,* 202–209. https://doi.org/10.3103/S0891416820040035

Ankaiah, D., Palanichamy, E., Antonyraj, C. B., Ayyanna, R., Perumal, V., Ahamed, S. I. B., & Arul, V. (2018). Cloning, overexpression, purification of bacteriocin enterocin-B and structural analysis, interaction determination of enterocin-A, B against pathogenic bacteria and human cancer cells. *International Journal of Biological Macromolecules*, *116*, 502-512. https://doi.org/10.1016/j.ijbiomac.2018.05.002

Aragón, F., Perdigón, G., de Moreno de LeBlanc, A. (2014). Modification in the diet can induce beneficial effects against breast cancer. *World Journal of Clinical Oncology*, *5*(3), 455-64. https://doi.org/10.5306/wjco.v5.i3.455

Aragon-Alegro, L. C., Alarcon Alegro, J. H., Roberta Cardarelli, H., Chih Chiu, M., & Isay Saad, S. M. (2007). Potentially probiotic and synbiotic chocolate mousse. *LWT-Food Science and Technology*, *40*, 669-675. https://doi.org/10.1016/j.lwt.2006.02.020

Arakawa, K., Kawai, Y., Iioka, H., Tanioka, M., Nishimura, J., Kitazawa, H., Tsurumi, K., & Saito, T. (2009). Effects of gassericins A and T, bacteriocins produced by *Lactobacillus gasseri*, with glycine on custard cream preservation. *Journal of Dairy Science*, *92*, 2365–2372. https://doi.org/10.3168/jds.2008-1240

Illippangama, A. U., Jayasena, D. D., Cheorun, J., & Mudannayake, D. C. (2022). Inulin as a functional ingredient and their applications in meat products. *Carbohydrate Polymers*, 275, 118706. https://doi.org/10.1016/j.carbpol.2021.118706

Astudillo-Melgar, F., Ochoa-Leyva, A., Utrilla, J., & Huerta-Beristain, G. (2019). Bacterial diversity and population dynamics during the fermentation of palm wine from Guerrero Mexico. *Frontiers in Microbiology*, *10*, 531. https://doi.org/10.3389/fmicb.2019.00531

Aymerich, T., Picouet, P. A., & Monfort, J. M. (2008). Decontamination technologies for meat products. *Meat Science*, *78*, 114–129. https://doi.org/10.1016/j.meatsci.2007.07.007

Baccouri, O., Boukerb, A. M., Farhat, L. B., Zébré, A., Zimmermann, K., Domann, E., Cambronel, M., Barreau, M., Maillot, O., Rincé, I., Muller, C., Marzouki, M. N., Feuilloley, M., Abidi, F., & Connil, N. (2019). Probiotic potential and safety evaluation of *Enterococcus faecalis* OB14 and OB15, isolated from traditional Tunisian testouri cheese and rigouta, using physiological and genomic analysis. *Frontiers in Microbiology*, *10*, 881. https://doi.org/10.3389/fmicb.2019.00881

Barefoot, S. F., Nettles, C. G., & Chen. Y. R. (1994). Lactacin B, a bacteriocin produced by *Lactobacillus acidophilus*. In: L. De Vuyst & E. J. Vandamme (Ed.), *Bacteriocins of lactic acid bacteria* (pp. 353-376). Springer, Boston, MA. https://doi.org/10.1007/978-1-4615-2668-1_13

Bartowsky, E. J., Costello, P. J., & Chambers, P. J. (2015). Emerging trends in the application of malolactic fermentation. *Australian Journal of Grape and Wine Research*, *21*, 663–669. https://doi.org/10.1111/ajgw.12185

Bastos, M. d. C. d. F., Coutinho, B. G., & Coelho, M. L. V. (2010). Lysostaphin: a staphylococcal bacteriolysin with potential clinical applications. *Pharmaceuticals (Basel), 3*, 1139-1161. https://doi.org/10.3390/ph3041139

Bindu, A., & Lakshmidevi, N. (2021). Identification and *in vitro* evaluation of probiotic attributes of lactic acid bacteria isolated from fermented food sources. *Archives of microbiology*, *203*(2), 579–595. https://doi.org/10.1007/s00203-020-02037-0

Bintsis, T. (2018a). Lactic acid bacteria: their applications in foods. *Journal of Bacteriology and Mycology*, *6*(2), 89–94. https://doi.org/10.15406/jbmoa.2018.06.00182

Bintsis, T. (2018b). Lactic acid bacteria as starter cultures: An update in their metabolism and genetics. *AIMS Microbiology*, *4*(4), 665–684. https://doi.org/10.3934/microbiol.2018.4.665

Biolcati, F., Andrighetto, C., Bottero, M. T., & Dalmasso, A. (2020). Microbial characterization of an artisanal production of Robiola di Roccaverano cheese. *Journal of Dairy Science*, *103*(5), 4056–4067. https://doi.org/10.3168/jds.2019-17451

Blaya, J., Barzideh, Z., & LaPointe, G. (2018). Symposium review: Interaction of starter cultures and nonstarter lactic acid bacteria in the cheese environment. *Journal of Dairy Science*, *101*(4), 3611-3629. https://doi.org/10.3168/jds.2017-13345

Brizuela, N., Tymczyszyn, E. E., Semorile, L. C., La Hens, D. V., Delfederico, L., Hollmann, A., & Bravo-Ferrada, B. (2018a). *Lactobacillus plantarum* as a malolactic starter culture in winemaking: A new (old) player? *Electronic Journal of Biotechnology*, https://doi.org/10.1016/j.ejbt.2018.12.002

Brizuela, N. S., Bravo-Ferrada, B. M., Curilén, Y., Delfederico, L., Caballero, A., & Semorile, L. (2018b). Advantages of using blend cultures of native *L. plantarum* and *O. oeni* strains to induce malolactic fermentation of Patagonian Malbec wine. *Frontiers in Microbiology*, *9*, 2109. https://doi.org/10.3389/fmicb.2018.02109

Cappello, M. S., Zapparoli, G., Logrieco, A., & Bartowsky, E. J. (2017). Linking wine lactic acid bacteria diversity with wine aroma and flavour. *International Journal of Food Microbiology, 243*, 16-27. https://doi.org/10.1016/j.ijfoodmicro.2016.11.025

Casaburi, A., Martino, V. D. I., Ferranti, P., Picariello, L., & Villani, F. (2016). Technological properties and bacteriocins production by *Lactobacillus curvatus* 54M16 and its use as starter culture for fermented sausage manufacture. *Food Control*, *59*, 31–45. https://doi.org/10.1016/j.foodcont.2015.05.016

Fontana, C., Cocconcelli, P. S., Vignolo, G., & Saavedra, L. (2015). Occurrence of antilisterial structural bacteriocins genes in meat borne lactic acid bacteria. *Food Control*, *47*, 53–59. https://doi.org/10.1016/j.foodcont.2014.06.021

Chaikaew, S., Baipong, S., Sone, T., Kanpiengjai, A., Chui-Chai, N., Asano, K., & Khanongnuch, C. (2017). Diversity of lactic acid bacteria from Miang, a traditional fermented tea leaf in northern Thailand and their tannin-tolerant ability in tea extract. *Journal of Microbiology* (Seoul, Korea), *55*(9), 720–729. https://doi.org/10.1007/s12275-017-7195-8

Chen, J., Lv, H., Zhang, Z., Zhang, H., Zhang, B., Wang, X., Liu, Y., Zhang, M., Pang, H., Qin, G., Wang, L., & Tan, Z. (2021). Multilocus sequence typing of *Leuconostoc mesenteroides* strains from the Qinghai-Tibet plateau. *Frontiers in Microbiology*, *12*, 614286. https://doi.org/10.3389/fmicb.2021.614286

Chen, Y. S., Liao, Y. J., Lan, Y. S., Wu, H. C., & Yanagida, F. (2017). Diversity of lactic acid bacteria associated with banana fruits in Taiwan. *Current microbiology*, *74*(4), 484–490. https://doi.org/10.1007/s00284-017-1213-2

Cheong, E. Y. L., Sandhu, A., Jayabalan, J., Le Kieu, T.T., Nhiep, N. T., My Ho, H. T., Zwielehner, J., Bansal, N., & Turner, M. S. (2014). Isolation of lactic acid bacteria with antifungal activity against the common cheese spoilage mould *Penicillium commune* and their potential as biopreservatives in cheese. *Food Control*, *46*, 91–97. https://doi.org/10.1016/j.foodcont.2014.05.011

Cho, Y. R., Chang, J. Y., & Chang, H. C. (2007). Production of gamma-aminobutyric acid (GABA) by *Lactobacillus buchneri* isolated from Kimchi and its neuroprotective effect on neuronal cells. *Journal of Microbiology and Biotechnology*, *17*, 104-109.

Chollet, M., Gille, D., Schmid, A., Walther, B., & Piccinali, P. (2013). Acceptance of sugar reduction in flavored yogurt. *Journal of Dairy Science*, *96*, 5501-5511. https://doi.org/10.3168/jds.2013-6610

Comasio, A., Verce, M., Van Kerrebroeck, S., & De Vuyst, L. (2020). Diverse microbial composition of sourdoughs from different origins. *Frontiers in Microbiology*, *11*, 1212. https://doi.org/10.3389/fmicb.2020.01212

Correia Santos, S., Fraqueza, M. João, Elias, M., Salvador Barreto, A., & Semedo-Lemsaddek, T. (2017). Traditional dry smoked fermented meat sausages: Characterization of autochthonous enterococci. *LWT - Food Science and Technology*, *79*, 410-415. https://doi.org/10.1016/j.lwt.2017.01.042

Cousin, F. J., Le Guellec, R., Chagnot, C., Goux, D., Dalmasso, M., Laplace, J. M., & Cretenet, M. (2019a). *Oenococcus sicerae* sp. nov., isolated from French cider. *Systematic and Applied Microbiology*, *42*(3), 302–308. https://doi.org/10.1016/j.syapm.2018.12.006

Cousin, F. J., Le Guellec, R., Chuat, V., Dalmasso, M., Laplace, J. M., & Cretenet, M. (2019b). Multiplex PCR for rapid identification of major lactic acid bacteria genera in cider and other fermented foods. *International Journal of Food Microbiology*, *291*, 17–24. https://doi.org/10.1016/j.ijfoodmicro.2018.11.004

Cruxen, C., Funck, G. D., Haubert, L., Dannenberg, G., Marques, J. L., Chaves, F. C., da Silva, W. P., & Fiorentini, Â. M. (2019). Selection of native bacterial starter culture in the production of fermented meat sausages: Application potential, safety aspects, and emerging technologies. *Food Research International* (Ottawa, Ont.), *122*, 371–382. https://doi.org/10.1016/j.foodres.2019.04.018

Cruz, A. G., Cavalcanti, R. N., Guerreiro. L. M. R., Sant'Ana, A. S., Nogueira, L.C., Oliveira, C. A. F., Deliza, R., Cunha, R. L., Faria, J. A. F., & Bolini, H. M. A. (2013). Developing a prebiotic yogurt: Rheological, physico-chemical and microbiological aspects and adequacy of survival analysis methodology. *Journal of Food Engineering*, *114*, 323-330. https://doi.org/10.1016/j.jfoodeng.2012.08.018

Daniali, M., Nikfar, S., & Abdollahi, M. (2020). Antibiotic resistance propagation through probiotics. *Expert Opinion on Drug Metabolism & Toxicology*, *16*(12), 1207–1215. https://doi.org/10.1080/17425255.2020.1825682

Das, J. D., Shankar, A., Johnson, J. B., & Thomas, S. (2020). Critical insights into antibiotic resistance transferability in probiotic *Lactobacillus*. *Nutrition*, *69*, 110567. https://doi.org/10.1016/j.nut.2019.110567

De Pasquale, I., Di Cagno, R., Buchin, S., De Angelis, M., & Gobbetti, M. (2019). Use of autochthonous mesophilic lactic acid bacteria as starter cultures for making Pecorino Crotonese cheese: Effect on compositional, microbiological and biochemical attributes. *Food Research International* (Ottawa, Ont.), *116*, 1344–1356. https://doi.org/10.1016/j.foodres.2018.10.024

Díaz-Muñoz, C., Van de Voorde, D., Comasio, A., Verce, M., Hernandez, C. E., Weckx, S., & De Vuyst, L. (2021). Curing of cocoa beans: fine-scale monitoring of the starter cultures applied and metabolomics of the fermentation and drying steps. *Frontiers in Microbiology*, *11*, 616875. https://doi.org/10.3389/fmicb.2020.616875

Dicks, L. M. T., Heunis, T. D. J., van Staden, D. A., Brand, A., Noll, K. S., & Chikindas, M. L. (2011) Medical and personal care applications of bacteriocins produced by lactic acid bacteria. In D. Drider & S. Rebuffat (Ed.), *Prokaryotic antimicrobial peptides* (pp. 391-421). Springer, New York, NY. https://doi.org/10.1007/978-1-4419-7692-5_19

Dong, Y., Zhang, F., Wang, B., Gao, J., Zhang, J., & Shao, Y. (2019). Laboratory evolution assays and whole-genome sequencing for the development and safety evaluation of *Lactobacillus plantarum* with stable resistance to gentamicin. *Frontiers in Microbiology*, *10*, 1235. https://doi.org/10.3389/fmicb.2019.01235

Dušková, M., Morávková, M., Mrázek, J., Florianová, M., Vorlová, L., & Karpíšková, R. (2020). Assessment of antibiotic resistance in starter and non-starter lactobacilli of food origin. *Acta Veterinaria Brno*, *89*, 401-411. https://doi.org/10.2754/avb202089040401

Dysvik, A., La Rosa, S. L., Liland, K. H., Myhrer, K. S., Østlie, H. M., De Rouck, G., Rukke, E-O., Westereng Bjørge, W., & Wicklund, T. (2020). Co-fermentation involving *Saccharomyces cerevisiae* and *Lactobacillus* species tolerant to brewing-related stress factors for controlled and rapid production of sour beer. *Frontiers in Microbiology, 11*, 279. https://doi.org/10.3389/fmicb.2020.00279

Endo, K., Mine, Y., Shuto, T., Taji, T., Murayama, T., & Nikawa, H. (2020). Comprehensive analysis of transcriptional profiles in oral epithelial-like cells stimulated with oral probiotic *Lactobacillus* spp. *Archives of Oral Biology*, *118*, 104832. https://doi.org/10.1016/j.archoralbio.2020.104832

Etayash, H., Norman, L., Thundat, T., Stiles, M., & Kaur, K. (2014). Surface-conjugated antimicrobial peptide leucocin a displays high binding to pathogenic gram-positive bacteria. *ACS Applied Materials & Interfaces*, *6*(2), 1131–1138. https://doi.org/10.1021/am404729c

EFSA BIOHAZ Panel (EFSA Panel on Biological Hazards), Koutsoumanis, K., Allende, A., Alvarez-Ordóñez, A., Bolton, D., Bover-Cid, S., Chemaly, M., Davies, R., De Cesare, A., Hilbert, F., Lindqvist, R., Nauta, M., Peixe, L., Ru, G., Simmons, M., Skandamis, P., Suffredini, E., Cocconcelli, P. S., Fernández Escámez, P. S., Maradona, M. P., Querol, A., Suarez, J. E., Sundh, I., Vlak, J., Barizzone, F., Correia, S., & Herman, L. (2020). Scientific Opinion on the update of the list of QPS-recommended biological agents intentionally added to food or feed as notified to EFSA (2017–2019). *EFSA Journal*, *18*(2), 5966. https://doi.org/10.2903/j.efsa.2020.5966

EFSA (European Food Safety Authority) (2018). Guidance on the characterisation of microorganisms used as feed additives or as production organisms. *EFSA Journal*, *16*(3), 5206. https://doi.org/10.2903/j.efsa.2018.5206

Ferir, G., Petrova, M. I., Andrei, G., Huskens, D., Hoorelbeke, B., Snoeck, R., Vanderleyden, J., Balzarini, J., Bartoschek, S., Brönstrup. M., Süssmuth, R. D., & Schols, D. (2013). The lantibiotic peptide labyrinthopeptin A1 demonstrates broad anti-HIV and anti-HSV activity with potential for microbicidal applications. *PLoS One*, *8*(5), e64010. https://doi.org/10.1371/journal.pone.0064010

Ferrocino, I., Bellio, A., Giordano, M., Macori, G., Romano, A., Rantsiou, K., Decastelli, L., & Cocolin, L. (2018). Shotgun metagenomics and volatilome profile of the microbiota of fermented sausages. *Applied and Environmental Microbiology*, *84*(3), e02120-17. https://doi.org/10.1128/AEM.02120-17

Figueroa-Hernández, C., Mota-Gutierrez, J., Ferrocino, I., Hernández-Estrada, Z. J., González-Ríos, O., Cocolin, L., & Suárez-Quiroz, M. L. (2019). The challenges and perspectives of the selection of starter cultures for fermented cocoa beans. *International Journal of Food Microbiology*, *301*, 41–50. https://doi.org/10.1016/j.ijfoodmicro.2019.05.

Flores, M. (2018). Understanding the implications of current health trends on the aroma of wet and dry cured meat products. *Meat Science, 144*, 53-61. https://doi.org/10.1016/j.meatsci.2018.04.016

Flores, M., & Toldrá, F. (2011). Microbial enzymatic activities for improved fermented meats. *Trends in Food Science & Technology, 22*(2-3), 81-90. https://doi.org/10.1016/j.tifs.2010.09.007

Flórez, A. B., Campedelli, I., Delgado, S., Alegría, Á., Salvetti, E., Felis, G. E., Mayo, B., & Torriani, S. (2016). Antibiotic susceptibility profiles of dairy *Leuconostoc*, analysis of the genetic basis of atypical resistances and transfer of genes *in vitro* and in a food matrix. *PLoS ONE, 11*(1), e0145203. https://doi.org/10.1371/journal.pone.0145203

Fontana, M. B. C., de Bastos, M. d.C. F., & Brandelli, A. (2006) Bacteriocins Pep5 and Epidermin inhibit *Staphylococcus epidermidis* adhesion to catheters*. Current Microbiology*, *52*(5), 350-353. https://doi.org/10.1007/s00284-005-0152-5

Fraga Cotelo, M., Perelmuter Schein, K., Giacaman Salvo, S. S., Zunino Abirad, P. M., & Carro Techera, S. B. (2013). Antimicrobial properties of lactic acid bacteria isolated from Uruguayan artisan cheese. *Food Science and Technology* (Campinas), *33*(4), 801–804. https://doi.org/10.1590/S0101-20612013000400029

Franciosa, I., Alessandria, V., Dolci, P., Rantsiou, K., & Cocolin, L. (2018). Sausage fermentation and starter cultures in the era of molecular biology methods. *International*

Journal of Food Microbiology, *279*, 26–32. https://doi.org/10.1016/j.ijfoodmicro.2018.04.038

Fraqueza M. J. (2015). Antibiotic resistance of lactic acid bacteria isolated from dry-fermented sausages. *International Journal of Food Microbiology*, *212*, 76–88. https://doi.org/10.1016/j.ijfoodmicro.2015.04.035

Fraqueza M. J., Patarata L., & Lauková A., (2016). Protective starter cultures and bacteriocins in fermented meats. In N. Zdolec (Ed.), *Fermented meat products: Health aspects* (pp. 228–269). CRC Press, NewYork.

Fraqueza, M. J., Laranjo, M., Elias, M., & Patarata, L. (2021). Microbiological hazards associated to salt and nitrite reduction in cured meat products: control strategies based on antimicrobial effect of natural ingredients and protective microbiota. *Current Opinion in Food Science*, *40*, 32-39. https://doi.org/10.1016/j.cofs.2020.10.027

Fritzenwanker, M., Kuenne, C., Billion, A., Hain, T., Zimmermann, K., Goesmann A., Chakraborty, T., & Domann, E. (2013). Complete genome sequence of the probiotic *Enterococcus faecalis* Symbioflor 1 Clone DSM 16431. *Genome Announcements, 1*(1), e00165-12. https://doi.org/10.1128/genomea.00165-12

Fusco, V., Quero, G. M., Poltronieri, P., Morea, M., & Baruzzi, F. (2019). Autochthonous and probiotic lactic acid bacteria employed for production of "Advanced Traditional Cheeses". *Foods* (Basel, Switzerland), *8*(9), 412. https://doi.org/10.3390/foods8090412

Gantzias, C., Lappa, I. K., Aerts, M., Georgalaki, M., Manolopoulou, E., Papadimitriou, K., De Brandt, E., Tsakalidou, E., & Vandamme, P. (2020). MALDI-TOF MS profiling of non-starter lactic acid bacteria from artisanal cheeses of the Greek island of Naxos.

International Journal of Food Microbiology, *323*, 108586. https://doi.org/10.1016/j.ijfoodmicro.2020.108586

Garcia-Burgos, M., Moreno-Fernandez, J., Alferez, M. J., Diaz-Castro, J., & Lopez-Aliaga, I. (2020). New perspectives in fermented dairy products and their health relevance *Journal of Functional Foods*, *72*, 104059. https://doi.org/10.1016/j.jff.2020.104059

García-Cano, I., Rocha-Mendoza, D., Ortega-Anaya, J., Wang, K., Kosmerl, E., & Jiménez-Flores, R. (2019). Lactic acid bacteria isolated from dairy products as potential producers of lipolytic, proteolytic and antibacterial proteins. *Applied Microbiology and Biotechnology, 103*(13), 5243-5257. https://doi.org/10.1007/s00253-019-09844-6

Garneau, J. E., & Moineau, S. (2011). Bacteriophages of lactic acid bacteria and their impact on milk fermentations. *Microbial Cell Factories*, *10*, 20. https://doi.org/10.1186/1475-2859-10-S1-S20

Gerner-Smidt, P., Besser, J., Concepción-Acevedo, J., Folster, J. P., Huffman, J., Joseph, L. A., Kucerova, Z., Nichols, M. C., Schwensohn, C. A., & Tolar, B. (2019). Whole genome sequencing: bridging one-health surveillance of foodborne diseases. *Frontiers in Public Health*, *7*, 172. https://doi.org/10.3389/fpubh.2019.00172

Gibson, G. R., Hutkins, R., Sanders, M. E., Prescott, S. L., Reimer, R. A., Salminen, S. J., Scott, K., Stanton, C., Swanson, K. S., Cani, P. D., Verbeke, K., & Reid, G. (2017). Expert consensus document: The international scientific association for probiotics and prebiotics (ISAPP) consensus statement on the definition and scope of prebiotics. *Nature Reviews Gastroenterology & Hepatology*, *14*, 491–502. https://doi.org/10.1038/nrgastro.2017.75

Grande, B. M. J., Pulido, R., Del Carmen, L. A. M., Gálvez, A., & Lucas, R. (2014). The cyclic antibacterial peptide enterocin AS-48: isolation, mode of action, and possible food applications. *International Journal of Molecular Science*, *15*(12), 22706-22727. https://doi.org/10.3390/ijms151222706

Grujović, M., Mladenović, K., & Čomić, L. (2021). The probiotic potential and evaluation of the safety aspect of *Enterococcus* sp. strains isolated from traditionally made Serbian cheese. *Veterinarski arhiv*, *91*(3), 319–328. https://doi.org/10.24099/vet.arhiv.0925

Grujović, M., Mladenović, K., Nikodijević, D., & Čomić, L. (2019a). Autochthonous lactic acid bacteria - presentation of potential probiotics application. *Biotechnology Letters*, *41*(11), 1319–1331. https://doi.org/10.1007/s10529-019-02729-8

Grujović, M., Mladenović, K., Žugić Petrović, T., & Čomić, L. (2019b). Assessment of the antagonistic potential and ability of biofilm formation of *Enterococcus* spp. isolated from Serbian cheese. *Veterinarski arhiv*, *89*(5), 653–667. https://doi.org/10.24099/vet.arhiv.0485

Güllüce, M., Karadayı, M., & Bariş, Ö. (2013). Bacteriocins: Promising antimicrobials. In A. Mendes-Vilas (Ed.), *Microbial pathogens and strategies for combating them: science, technology and education* (pp. 1016–1027). Formatex, Madrid, Spain.

Guo, H., Pan, L., Li, L., Lu, J., Kwok, L., Menghe, B., Zhang, H., & Zhang, W. (2017). Characterization of antibiotic resistance genes from *Lactobacillus* isolated from traditional dairy products. *Journal of Food Science*, *82*(3), 724-730. https://doi.org/10.1111/1750-3841.13645

Guo, Z., Wang, Y., Xiang, F., Hou, Q., & Zhang, Z. (2021). Bacterial diversity in pickled cowpea (*Vigna unguiculata* [Linn.] Walp) as determined by illumina MiSeq sequencing and culture-dependent methods. *Current Microbiology*, *78*, 1286–1297. https://doi.org/10.1007/s00284-021-02382-3

Hajigholizadeh, M., Mardani, K., Moradi, M., & Jamshidi, A. (2020). Molecular detection, phylogenetic analysis, and antibacterial performance of lactic acid bacteria isolated from traditional cheeses, North-West Iran. *Food Science & Nutrition*, *8*(11), 6007–6013. https://doi.org/10.1002/fsn3.1887

Halim, M., Mustafa, N. A. M., Othman, M., Wasoh, H., Kapri, M. R., & Ariff, A. B. (2017). Effect of encapsulant and cryoprotectant on the viability of probiotic *Pediococcus acidilactici* ATCC 8042 during freeze-drying and exposure to high acidity, bile salts and heat. *LWT-Food Science and Technology, 81*, 210–216. https://doi.org/10.1016/j.lwt.2017.04.009

Han, Q., Kong, B. H., Chen, Q., Sun, F. D., & Zhang, H. (2017). *In vitro* comparison of probiotic properties of lactic acid bacteria isolated from Harbin dry sausages and selected probiotics. *Journal of Functional Foods*, *32*, 391–400. https://doi.org/10.1016/j.jff.2017.03.020

Harutoshi, T. (2013). *Exopolysaccharides of lactic acid bacteria for food and colon health applications*. Lactic acid bacteria – R&D for food, health and livestock purposes. IntechOpen.

Hayaloglu, A. A. (2016). *Cheese: Microbiology of cheese*. Reference Module in Food Sciences, Elsevier. http://dx.doi.org/10.1016/B978-0-08-100596-5.00675-2

Hekmat, S., & Reid, G. (2006). Sensory properties of probiotic yogurt is comparable to standard yogurt. *Nutrition Research*, *26*(4), 163-166. https://doi.org/10.1016/j.nutres.2006.04.004

Henning, C., Gautam, D., & Muriana, P. (2015). Identification of multiple bacteriocins in *Enterococcus* spp. using an *Enterococcus*-specific bacteriocin PCR array. *Microorganisms*, *3*, 1–16. https://doi.org/10.3390/microorganisms3010001

Heredia-Castro, P. Y., Méndez-Romero, J. I., Hernández-Mendoza, A., Acedo-Félix, E., González-Córdova, A. F., & Vallejo-Cordoba, B. (2015). Antimicrobial activity and partial characterization of bacteriocin-like inhibitory substances produced by *Lactobacillus* spp. isolated from artisanal Mexican cheese. *Journal of Dairy Science*, *98*(12), 8285–8293. https://doi.org/10.3168/jds.2015-10104

Hill, C., Guarner, F., Reid, G., Gibson, G. R., Merenstein, D. J., Pot, B., Morelli, L., Berni Canani, R., Flint, H. J., Salminen, S., Calder, P. C., & Sanders, M. E. (2014). The International Scientific Association for Probiotics and Prebiotics consensus statement on the scope and appropriate use of the term probiotic. *Nature Reviews Gastroenterology & Hepatology*, *11*, 506–514. https://doi.org/10.1038/nrgastro.2014.66

Ho, V. T. T., Fleet, G. H., & Zhao, J. (2018). Unravelling the contribution of lactic acid bacteria and acetic acid bacteria to cocoa fermentation using inoculated organisms. *International Journal of Food Microbiology*, *279*, 43-56. https://doi.org/10.1016/j.ijfoodmicro.2018.04.040

Hoppert, K., Zahn, S., Jänecke, L., Mai, R., Hoffmann, S., & Rohm, H. (2013). Consumer acceptance of regular and reduced-sugar yogurt enriched with different types of dietary fiber. *International Dairy Journal*, *28*, 1-7. https://doi.org/10.1016/j.idairyj.2012.08.005

Hurtado, A., Reguant, C., Bordons, A., & Rozès, N. (2012). Lactic acid bacteria from fermented table olives. *Food Microbiology, 31*(1), 1-8. doi:https://doi.org/10.1016/j.fm.2012.01.006

Iorizzo, M., Pannella, G., Lombardi, S. J., Ganassi, S., Testa, B., Succi, M., Sorrentino, E., Petrarca, S., De Cristofaro, A., Coppola, R., & Tremonte, P. (2020). Inter- and Intra-species diversity of lactic acid bacteria in *Apis mellifera ligustica* colonies. *Microorganisms*, *8*(10), 1578. https://doi.org/10.3390/microorganisms8101578

Jafari-Nasab, T., Khaleghi, M., Farsinejad, A., & Khorrami, S. (2021). Probiotic potential and anticancer properties of *Pediococcus* sp. isolated from traditional dairy products. *Biotechnology Reports* (Amsterdam, Netherlands), *29*, e00593. https://doi.org/10.1016/j.btre.2021.e00593

Jaimee, G., & Halami, P. M. (2016). High level aminoglycoside resistance in *Enterococcus*, *Pediococcus* and *Lactobacillus* species from farm animals and commercial meat products. *Annals of Microbiology*, *66*, 101–110. https://doi.org/10.1007/s13213-015-1086-1

Jampaphaeng, K., Cocolin, L., & Maneerat, S. (2017). Selection and evaluation of functional characteristics of autochthonous lactic acid bacteria isolated from traditional fermented stinky bean (Sataw-Dong). *Annals of Microbiology, 67*, 25–36. https://doi.org/10.1007/s13213-016-1233-3

Jarocki, P., Komoń-Janczara, E., Glibowska, A., Dworniczak, M., Pytka, M., Korzeniowska-Kowal, A., Wzorek, A., & Kordowska-Wiater, M. (2020). Molecular routes to specific identification of the *Lactobacillus casei* group at the species, subspecies and strain level. *International Journal of Molecular Science*, *21*(8), 2694. https://doi.org/10.3390/ijms21082694

Joerger, M. C., & Klaenhammer, T. R. (1986) Characterization and purification of helveticin J and evidence for a chromosomally determined bacteriocin produced by *Lactobacillus helveticus* 481. *Journal of Bacteriology*, *167*, 439-446. https://doi.org/10.1128/jb.167.2.439-446.1986

Jofré, A., Aymerich, T., Monfort, J. M., & Garriga, M. (2008). Application of enterocins A and B, sakacin K and nisin to extend the safe shelf-life of pressurized ready-to-eat meat products. *European Food Research and Technology*, *228*, 159–162. https://doi.org/10.1007/s00217-008-0913-z

Jørgensen, C. E., Abrahamsen, R. K., Rukke, E-O., Hoffmann, T. K., Johansen, A-G., & Skeie, S. B. (2019). Processing of high-protein yoghurt – A review. *International Dairy Journal*, *88*, 42-59. https://doi.org/10.1016/j.idairyj.2018.08.002

Kadri, Z., Spitaels, F., Cnockaert, M., Amar, M., Joossens, M., & Vandamme, P. (2021). The bacterial diversity of raw Moroccon camel milk. *International Journal of Food Microbiology*, *341*, 109050. https://doi.org/10.1016/j.ijfoodmicro.2021.109050

Kashyap, D. R. (2019). Microbial metabolites: Peptides of diverse structure and function. In V. Kumar Gupta, & A. Pandey (Ed.), *New and future developments in microbial biotechnology and bioengineering* (pp. 87-101). Elsevier. https://doi.org/10.1016/B978-0-444-63504-4.00007-4

Kazou, M., Grafakou, A., Tsakalidou, E., & Georgalaki, M. (2021). Zooming into the microbiota of home-made and industrial kefir produced in greece using classical microbiological and amplicon-based metagenomics analyses. *Frontiers in Microbiology*, 12, 621069. https://doi.org/10.3389/fmicb.2021.621069

Khan, S., Moore, R. J., Stanley, D., Chousalkar, K. K. (2020). Gut microbiota of laying hens and its manipulation with prebiotics and probiotics to enhance gut health and food safety. *Applied and Environmental Microbiology*, *86*(13), https://doi.org/10.1128/AEM.00600-20

Khochamit, N., Siripornadulsil, S., Sukon, P., & Siripornadulsil, W. (2015) Antibacterial activity and genotypic–phenotypic characteristics of bacteriocin-producing *Bacillus subtilis* KKU213: Potential as a probiotic strain. *Microbiological Research*, *170*, 36-50. https://doi.org/10.1016/j.micres.2014.09.004

Kim, E., Cho, E. J., Yang, S. M., Kim, M. J., & Kim, H. Y. (2021). Novel approaches for the identification of microbial communities in kimchi: MALDI-TOF MS analysis and high-throughput sequencing. *Food Microbiology*, *94*, 103641. https://doi.org/10.1016/j.fm.2020.103641

Kim, E., Yang, S. M., Cho, E. J., & Kim, H. Y. (2020). Novel real-time PCR assay for *Lactobacillus casei* group species using comparative genomics. *Food Microbiology*, *90*, 103485. https://doi.org/10.1016/j.fm.2020.103485

Kochan, P., Chmielarczyk, A., Szymaniak, L., Brykczynski, M., Galant, K., Zych, A., Pakosz, K., Giedrys-Kalemba, S., Lenouvel, E., & Heczko. P. B. (2011). *Lactobacillus rhamnosus* administration causes sepsis in a cardiosurgical patient--is the time right to revise probiotic safety guidelines? *Clinical Microbiology and Infection*, *17*(10), 1589-1592. https://doi.org/10.1111/j.1469-0691.2011.03614.x

Konkit, M., & Kim, W. (2016). Activities of amylase, proteinase, and lipase enzymes from *Lactococcus chungangensis* and its application in dairy products. *Journal of Dairy Science, 99*(7), 4999-5007. https://doi.org/10.3168/jds.2016-11002

Kook, S. Y., Chung, E. C., Lee, Y., Lee, D. W., & Kim, S. (2019). Isolation and characterization of five novel probiotic strains from Korean infant and children faeces. *PLoS ONE*, *14*(10), e0223913. https://doi.org/10.1371/journal.pone.0223913

Korcz, E., Kerényi, Z., & Varga, L. (2018). Dietary fibers, prebiotics, and exopolysaccharides produced by lactic acid bacteria: Potential health benefits with special regard to cholesterol-lowering effects. *Food & Function*, *9*(6), 3057–3068. https://doi.org/10.1039/c8fo00118a

Laranjo, M., Elias, M., & Fraqueza, M. J. (2017). The use of starter cultures in traditional meat products. *Journal of Food Quality, 2017*, 1-18. https://doi.org/10.1155/2017/9546026

Laranjo, M., Potes, M. E., & Elias, M. (2019). Role of starter cultures on the safety of fermented meat products. *Frontiers in Microbiology, 10*(853). https://doi.org/10.3389/fmicb.2019.00853

Lasagno, M., Navarro, M. d. l. A., Moliva, M., & Reinoso, E. (2019). Screening of bacteriocin associated genes of *Streptococcus uberis* strains. *Heliyon*, *5*(9), e02393. https://doi.org/10.1016/j.heliyon.2019.e02393

Lee, J. H., Shin, D., Lee, B., Lee, H., Lee, I., & Jeong, D. W. (2017). Genetic diversity and antibiotic resistance of *Enterococcus faecalis* isolates from traditional Korean fermented soybean foods. *Journal of Microbiology and Biotechnology*, *27*(5), 916–924. https://doi.org/10.4014/jmb.1612.12033

Leeuwendaal, N., Stanton, C., O'Toole, P. W., & Beresford, T. P. (2021). The potential of non-starter lactic acid bacteria from Cheddar cheese to colonise the gut. *Journal of Functional Foods*, *83*, https://doi.org/10.1016/j.jff.2021.104425

Leite, A. M. O., Miguel, M. A. L., Peixoto, R. S., Ruas-Madiedo, P., Paschoalin, V. M. F., Mayo, B., & Delgado, S. (2015). Probiotic potential of selected lactic acid bacteria strains isolated from Brazilian kefir grains. *Journal of Dairy Science, 98*(6), 3622-3632. https://doi.org/10.3168/jds.2014-9265

Lengkey H. A. W., & Balia R. L. (2014). The effect of starter dosage and fermentation time on pH and lactic acid production. *Biotechnology in Animal Husbandry*, *30*(2), 339-347. https://doi.org/10.2298/BAH1402339L

Li, T., Teng, D., Mao, R., Hao, Y., Wang, X., & Wang, J. (2020). A critical review of antibiotic resistance in probiotic bacteria. *Food Research International* (Ottawa, Ont.), *136*, 109571. https://doi.org/10.1016/j.foodres.2020.109571

López-Seijas, J., García-Fraga, B., da Silva, A. F., Zas-García, X., Lois, L. C., Gago-Martínez, A., Leão-Martins, J. M., & Sieiro, C. (2020). Evaluation of malolactic bacteria associated with wines from Albariño variety as potential starters: Screening for quality and safety. *Foods* (Basel, Switzerland), *9*(1), 99. https://doi.org/10.3390/foods9010099

Luiz, L. M., Chuat, V., Madec, M. N., Araújo, E. A., de Carvalho, A. F., & Valence, F. (2016). Mesophilic lactic acid bacteria diversity encountered in Brazilian farms producing milk with particular interest in *Lactococcus lactis* strains. *Current Microbiology*, *73*(4), 503–511. https://doi.org/10.1007/s00284-016-1086-9

Makhloufi, K. M., Carré-Mlouka, A., Peduzzi, J., Lombard, C., van Reenen C. A., Milner, L., Dicks, T., & Rebuffat, S. (2013). Characterization of leucocin B-KM432Bz from *Leuconostoc pseudomesenteroides* isolated from Boza, and comparison of its efficiency to Pediocin PA-1. *PLoS One*, *8*(8), e70484. https://doi.org/10.1371/journal.pone.0070484

Mannaa, M., Seo, Y. S., & Park, I. (2019). Effect of seafood (gizzard shad) supplementation on the chemical composition and microbial dynamics of radish kimchi during fermentation. *Scientific Reports*, *9*(1), 17693. https://doi.org/10.1038/s41598-019-54318-4

Mao, B., & Yan, S. (2019). Lactic acid bacteria and fermented fruits and vegetables. In W. Chen (Ed.), *Lactic acid bacteria* (pp. 181-209). Springer, Singapore. https://doi.org/10.1007/978-981-13-7283-4_7

Marco, M. L., Heeney, D., Binda, S., Cifelli, C. J., Cotter, P. D., Foligné, B., Gänzle, M., Kort, R., Pasin, G., Pihlanto, A., Smid, E. J., & Hutkins, R. (2017). Health benefits of fermented foods: microbiota and beyond. *Current Opinion in Biotechnology, 44*, 94-102. https://doi.org/10.1016/j.copbio.2016.11.010

Markowiak, P., & Śliżewska, K. (2017). Effects of probiotics, prebiotics, and synbiotics on human health. *Nutrients*, *9*(9), 1021. https://doi.org/10.3390/nu9091021

Martins, W. F., Longhi, D. A., de Aragão, G., Melero, B., Rovira, J., & Diez, A. M. (2020). A mathematical modelling approach to the quantification of lactic acid bacteria in vacuum-packaged samples of cooked meat: Combining the TaqMan-based quantitative PCR method with the plate-count method. *International Journal of Food Microbiology*, *318*, 108466. https://doi.org/10.1016/j.ijfoodmicro.2019.108466

Mastanjevic, K., Kovacevic, D., Frece, J., Markov, K., & Pleadin, J. (2017). The effect of autochthonous starter culture, sugars, and temperature on the fermentation of Slavonian Kulen. *Food Technology and Biotechnology*, *55*, 67–76. https://doi.org/10.17113/ftb.55.01.17.4688

Mbye, M., Affan Baig, M., AbuQamar, S. F., El-Tarabily, K. A., Obaid, R. S., Osaili, T. M., Al-Nabulsi, A. A., Turner, M. S., Shah, N. P., & Ayyash, M. M. (2020). Updates on understanding of probiotic lactic acid bacteria responses to environmental stresses and highlights on proteomic analyses. *Comprehensive Reviews in Food Science and Food Safety*, *19*(3), 1110-1124. https://doi.org/10.1111/1541-4337.12554

McCain, H. R., Kaliappan, S., & Drake, M. A. (2018). Invited review: Sugar reduction in dairy products. *Journal of Dairy Science*, *101*(10), 8619-8640. https://doi.org/10.3168/jds.2017-14347

Medina-Pradas, E., Pérez-Díaz, M. I., Garrido-Fernández, A., & Arroyo-López, F. N. (2017). Review of vegetable fermentations with particular emphasis on processing modifications, microbial ecology, and spoilage. In A. Bevilacqua, M. A. Corbo, & M. Sinigaglia (Ed.), *The microbiological quality of food* (pp. 211-236). Woodhead Publishing. https://doi.org/10.1016/B978-0-08-100502-6.00012-1

Miranda-Castilleja, D. E., Martínez-Peniche, R. Á, Aldrete-Tapia, J. A., Soto-Muñoz, L., Iturriaga, M. H., & Pacheco-Aguilar, J. R. (2016). Distribution of native lactic acid bacteria in wineries of Queretaro, Mexico and their resistance to wine-like conditions. *Frontiers in Microbiology*, *7,* 1769. https://doi.org/10.3389/fmicb.2016.01769

Mokoena, M. P., Mutanda, T., & Olaniran, A. O. (2016). Perspectives on the probiotic potential of lactic acid bacteria from African traditional fermented foods and beverages. *Food & Nutrition Research*, *60*, 29630. https://doi.org/10.3402/fnr.v60.29630

Moreno, I., Marasca, E. T. G., de Sá, P. B. Z. R., de Souza Moitinho, J., Gonçalves Marquezini, M., Alves, M. R. C., & Bromberg, R. (2018). Evaluation of probiotic potential of bacteriocinogenic lactic acid bacteria strains isolated from meat products. *Probiotics and Antimicrobial Proteins*, *10*, 762–774. https://doi.org/10.1007/s12602-018-9388-9

Morisset, D., Berjeaud, J. M., Marion, D., Lacombe, C., & Frère, J. (2004). Mutational analysis of Mesentericin Y105, an anti-*Listeria* bacteriocin, for determination of impact on bactericidal activity, *in vitro* secondary structure, and membrane interaction.

Applied and Environmental Microbiology, *70*, 4672-4680. https://doi.org/10.1128/AEM.70.8.4672-4680.2004

Motahari, P., Mirdamadi, S., & Kianirad, M. (2017). Safety evaluation and antimicrobial properties of *Lactobacillus pentosus* 22C isolated from traditional yogurt. *Journal of Food Measurement and Characterization*, *11*, 972-978. https://doi.org/10.1007/s11694-017-9471-z

Motey, G. A., Owusu-Kwarteng, J., Obiri-Danso, K., Ofori, L. A., Ellis, W. O., & Jespersen, L. (2021). *In vitro* properties of potential probiotic lactic acid bacteria originating from Ghanaian indigenous fermented milk products. *World Journal of Microbiology & Biotechnology*, *37*(3), 52. https://doi.org/10.1007/s11274-021-03013-6

Mrkonjic Fuka, M., Tanuwidjaja, I., Zgomba Maksimović, A., Zunabovic-Pichler, M., Kublik, S., Hulak, N., Domig, K. J., & Schloter, M. (2020). Bacterial diversity of naturally fermented game meat sausages: Sources of new starter cultures. *LWT-Food Science and Technology*, *118*, https://doi.org/10.1016/j.lwt.2019.108782

Munekata, P. E. S., Pateiro, M., Zhang, W., Domínguez, R., Xing, L., Fierro, E. M., & Lorenzo, J. M. (2020). Autochthonous probiotics in meat products: selection, identification, and their use as starter culture. *Microorganisms*, *8*, 1833; https://doi.org/10.3390/microorganisms8111833

Muruzović, M., Mladenović, K., Žugić Petrović, T., & Čomić, L. (2018a). Characterization of lactic acid bacteria isolated from traditionally made Serbian cheese and evaluation of their antagonistic potential against Enterobacteriaceae. *Journal of Food Processing and Preservation*, *42*(4), 1–9. https://doi.org/10.1111/jfpp.13577

Muruzović, M., Mladenović, K., Đilas, M., Stefanović, O., & Čomić, L. (2018b). *In vitro* evaluation of antimicrobial potential and ability of biofilm formation of autochthonous

Lactobacillus spp. and *Lactococcus* spp. isolated from traditionally made cheese from Southeastern Serbia. *Journal of Food Processing and Preservation*, *42*(11), 1–10. https://doi.org/10.1111/jfpp.13776

Muruzović, M., Mladenović, K., & Čomić, L. (2018c). *In vitro* evaluation of resistance to environmental stress by planktonic and biofilm form of lactic acid bacteria isolated from traditionally made cheese from Serbia. *Food Bioscience*, *23*, 54–59. https://doi.org/10.1016/j.fbio.2018.03.005

Nakayama, J., Tanaka, E., Kariyama, R., Nagata, K., Nichiguchi, K., Mitsuhata, R., Uemura, Y., Tanokura, M, Kumon, H., & Sonomoto, K. (2007). Siamycin attenuates fsr quorum sensing mediated by a gelatinase biosynthesis-activating pheromone in *Enterococcus faecalis. Journal of Bacteriology*, *189*(4):1358-65. https://doi.org/10.1128/JB.00969-06

Nethery, M. A., Henriksen, E. D., Daughtry, K. V., Johanningsmeier, S. D., & Barrangou, R. (2019). Comparative genomics of eight *Lactobacillus buchneri* strains isolated from food spoilage. *BMC Genomics*, *20*(1), 902. https://doi.org/10.1186/s12864-019-6274-0

Neumann, B., Prior, K., Bender, J. K., Harmsen, D., Klare, I., Fuchs, S., Bethe, A., Zühlke, D., Göhler, A., Schwarz, S., Schaffer, K., Riedel, K., Wieler, L. H., & Werner, G. (2019). A core genome multilocus sequence typing scheme for *Enterococcus faecalis*. *Journal of Clinical Microbiology*, *57*(3), e01686-18. https://doi.org/10.1128/JCM.01686-18

Newstead L. N., Varjonen, K., Nuttall, T., & Paterson, G. K. (2020). Staphylococcal-produced bacteriocins and antimicrobial peptides: Their potential as alternative treatments for *Staphylococcus aureus* infections. *Antibiotics* (Basel), *9*(2), 40. https://doi.org/10.3390/antibiotics9020040

Nguyen, N. K., Dong, N. T. N., Nguyen, H. T., & Le, P. H. (2015). Lactic acid bacteria: promising supplements for enhancing the biological activities of kombucha. *SpringerPlus, 4*(1). https://doi.org/10.1186/s40064-015-0872-3

Nkhata, S. G., Ayua, E., Kamau, E. H., & Shingiro, J. B. (2018). Fermentation and germination improve nutritional value of cereals and legumes through activation of endogenous enzymes. *Food Science & Nutrition*, *6*, 2446–2458. https://doi.org/10.1002/fsn3.846

O'Donnell, S. T., Ross, R. P., & Stanton, C. (2020). The progress of multi-omics technologies: determining function in lactic acid bacteria using a systems level approach. *Frontiers in Microbiology*, *10*, 3084. https://doi.org/10.3389/fmicb.2019.03084

Ojha, A. K., Shah, N. P., & Mishra, V. (2021). Conjugal transfer of antibiotic resistances in *Lactobacillus* spp. *Current Microbiology, 78,* 2839–2849. https://doi.org/10.1007/s00284-021-02554-1

Oleksy, M., & Klewicka, E. (2018). Exopolysaccharides produced by *Lactobacillus* sp.: Biosynthesis and applications. *Critical Reviews in Food Science and Nutrition*, *58*(3), 450–462. https://doi.org/10.1080/10408398.2016.1187112

Oliveira, L. B., & Jurkiewicz, C. H. (2009). Influence of inulin and acacia gum on the viability of probiotic bacteria in synbiotic fermented milk. *Brazilian Journal of Food Technology*, *12*(2), 138-144. https://doi.org/10.4260/BJFT20095808

Ong, L., Henriksson, A., & Shah, N. P. (2007). Angiotensin converting enzyme-inhibitory activity in Cheddar cheeses made with the addition of probiotic *Lactobacillus casei* sp. *Le Lait, INRA Editions, 87*, 149-165. https://hal.archives-ouvertes.fr/hal-00895638/document

Özogul, F., & Hamed, I. (2017). The importance of lactic acid bacteria for the prevention of bacterial growth and their biogenic amines formation: A review. *Critical Reviews in Food Science and Nutrition*, *58*(10), 1660-1670. https://doi.org/10.1080/10408398.2016.1277972

Papadimitriou, K., Alegria, A., Bron, P. A., De Angelis, M., Gobbetti, M., Kleerebezem, M., Lemos, J. A., Linares, D. M., Ross, P., Stanton, C., Turroni, F., van Sinderen, D., Varmanen, P., Ventura, M., Zúñiga, M., Tsakalidou, E., & Kok, J. (2016). Stress physiology of lactic acid bacteria. *Microbiology and Molecular Biology Reviews*, *80*(3), 837-890. https://doi.org/10.1128/MMBR.00076-15

Park, J., Jin, G. D., Pak, J. I., Won, J., & Kim, E. B. (2017). Development of a rapid identification method for the differentiation of *Enterococcus* species using a species-specific multiplex PCR based on comparative genomics. *Current Microbiology*, *74*(4), 476–483. https://doi.org/10.1007/s00284-017-1210-5

Patten, D. A., & Laws, A. P. (2015). Lactobacillus-produced exopolysaccharides and their potential health benefits: A review. *Beneficial Microbes*, *6*, 457-471. https://doi.org/10.3920/BM2014.0117

Penido, F., Piló, F. B., Sandes, S., Nunes, Á. C., Colen, G., Oliveira, E. S., Rosa, C. A., & Lacerda, I. (2018). Selection of starter cultures for the production of sour cassava starch in a pilot-scale fermentation process. *Brazilian Journal of Microbiology*, *49*(4), 823–831. https://doi.org/10.1016/j.bjm.2018.02.001

Pérez-Díaz, I. M., Johanningsmeier, S. D., Anekella, K., Pagán-Medina, C. G., Méndez-Sandoval, L., Arellano, C., Price, R., Daughtry, K. V., Borges, M., Bream, C., Connelly, L., Dieck, S. E., Levi, M. T., McMurtrie, E. K., Smith, R. E., Jr, Theora, J. C., Wendland, P., Gómez-Rodríguez, F., & Arroyo-López, F. N. (2021). Genotypic and phenotypic diversity among *Lactobacillus plantarum* and *Lactobacillus pentosus* isolated from industrial scale cucumber fermentations. *Food Microbiology*, *94*, 103652. https://doi.org/10.1016/j.fm.2020.103652

Pintado, C. M. B. S., Ferreira, M. A. S. S., & Sousa, I. (2010). Control of pathogenic and spoilage microorganisms from cheese surface by whey protein films containing malic acid, nisin and natamycin. *Food Control*, *21*, 240–246. https://doi.org/10.1016/j.foodcont.2009.05.017

Pisano, M. B., Fadda, M. E., Melis, R., Ciusa, M. L., Viale, S., Deplano, M., & Cosentino, S. (2015). Molecular identification of bacteriocins produced by *Lactococcus lactis* dairy strains and their technological and genotypic characterization. *Food Control*, *51*, 1–8. https://doi.org/10.1016/j.foodcont.2014.11.005

Pradhan, P., & Tamang, J. P. (2019). Phenotypic and genotypic identification of bacteria isolated from traditionally prepared dry starters of the Eastern Himalayas. *Frontiers in Microbiology*, *10*, 2526. https://doi.org/10.3389/fmicb.2019.02526

Qin, Y., Wang, Y., He, Y., Zhang, Y., She, Q., Chai, Y., Li, P., Shang, Q. (2019). Characterization of Subtilin L-Q11, a novel class I bacteriocin synthesized by *Bacillus subtilis* L-Q11 isolated from orchard soil. *Frontiers in Microbiology*, https://doi.org/10.3389/fmicb.2019.00484

Quinto, E. J., Miguel Marin, J., & Schaffner, D. (2016) Effect of the competitive growth of *Lactobacillus sakei* MN on the growth kinetics of *Listeria monocytogenes* Scott A in model meat gravy. *Food Control*, *63*, 34-45. https://doi.org/10.1016/j.foodcont.2015.11.025

Rammelsberc, M., & Radler, F. (1990). Antibacterial polypeptides of *Lactobacillus* species. *Journal of Applied Bacteriology*, *69*(2), 177-184. https://doi.org/10.1111/j.1365-2672.1990.tb01507.x

Ramos, C. L., Thorsen, L., Schwan, R. F., & Jespersen, L. (2013). Strain-specific probiotics properties of *Lactobacillus fermentum*, *Lactobacillus plantarum* and *Lactobacillus brevis* isolates from Brazilian food products. *Food Microbiology*, *36*, 22–29. https://doi.org/10.1016/j.fm.2013.03.010

Ranadheera, C.S., Vidanarachchi, J. K., Rocha, R. S., Cruz, A. G., & Said Ajlouni, S. (2017). Probiotic delivery through fermentation: Dairy vs. Non-Dairy Beverages. *Fermentation*, *3*, 67. https://doi.org/10.3390/fermentation3040067

Ray, R. C., & Joshi, V. K. (2015). Fermented foods: Past, present and future. In: R. C. Ray, & M. Didier (Ed.), *Microorganisms and fermentation of traditional foods* (pp. 1-36). Boca Raton: CRC Press. https://doi.org/10.1201/b17307

Rea, M. C., Sit, C. S., Clayton, E., O'Connor, P. M., Whittal, R. M., Zheng, J., Vederas, J. C., Paul Ross, R., & Hill, C. (2010). Thuricin CD, a posttranslationally modified bacteriocin with a narrow spectrum of activity against *Clostridium difficile*. *Proceedings of the National Academy of Sciences*, *107*(20), 9352-9357. https://doi.org/10.1073/pnas.0913554107

Ribeiro, S. C., O’Connor, P. M., Ross, R. P., Stanton, C., & Silva, C. C. (2016). An anti-listerial *Lactococcus lactis* strain isolated from Azorean Pico cheese produces lacticin 481. *International Dairy Journal*, *63*, 18–28. https://doi.org/10.1016/j.idairyj.2016.07.017

Rodrigo-Torres, L., Yépez, A., Aznar, R., & Arahal, D. R. (2019). Genomic insights into five strains of *Lactobacillus plantarum* with biotechnological potential isolated from chicha, a traditional maize-based fermented beverage from Northwestern Argentina. *Frontiers in Microbiology*, *10*, 2232. https://doi.org/10.3389/fmicb.2019.02232

Rodrigues, D., Rocha-Santos, T. A. P., Pereira, C. I., Gomes, A. M., Malcata, F. X., & Freitas, A. C. (2011). The potential effect of FOS and inulin upon probiotic bacterium performance in curdled milk matrices. *LWT - Food Science and Technology*, *44*, 100-108. https://doi.org/10.1016/j.lwt.2010.05.021

Routray, W., & Mishra, H. N. (2011). Scientific and technical aspects of yogurt aroma and taste: A Review. *Comprehensive Reviews in Food Science and Food Safety*, *10*(4), 208-220. https://doi.org/10.1111/j.1541-4337.2011.00151.x

Russo, N., Caggia, C., Pino, A., Coque, T. M., Arioli, S., & Randazzo, C. L. (2018). *Enterococcus* spp. in Ragusano PDO and Pecorino Siciliano cheese types: A snapshot of their antibiotic resistance distribution. *Food and Chemical Toxicology*, *120*, 277–286. https://doi.org/10.1016/j.fct.2018.07.023

Ryan, P. M., Ross, R. P., Fitzgerald, G. F., & Caplice, N. M. (2015). Stanton C. Sugar-coated: Exopolysaccharide producing lactic acid bacteria for food and human health applications. *Food & Function*, *6*(3), 679-693. https://doi.org/10.1039/c4fo00529e

Sáez, G. D., Flomenbaum, L., & Zárate, G. (2018). Lactic acid bacteria from Argentinean fermented foods: isolation and characterization for their potential use as starters for fermentation of vegetables. *Food Technology and Biotechnology*, *56*(3), 398–410. https://doi.org/10.17113/ftb.56.03.18.5631

Salaün, F., Mietton, B., & Gaucheron, F. (2005). Buffering capacity of dairy products. *International Dairy Journal*, *15*(2), 95-109. https://doi.org/10.1016/j.idairyj.2004.06.007

Sánchez-Juanes, F., Teixeira-Martín, V., González-Buitrago, J. M., Velázquez, E., & Flores-Félix, J. D. (2020). Identification of species and subspecies of lactic acid bacteria present in Spanish cheeses type "Torta" by MALDI-TOF MS and *pheS* gene analyses. *Microorganisms*, *8*(2), 301. https://doi.org/10.3390/microorganisms8020301

Scatassa, M. L., Gaglio, R., Cardamone, C., Macaluso, G., Arcuri, L., Todaro, M., & Mancuso, I. (2017). Anti-*Listeria* activity of lactic acid bacteria in two traditional Sicilian cheeses. *Italian Journal of Food Safety*, *5*, 13-17. https://doi.org/10.4081/ijfs.2017.6191

Schneidera, N., Werkmeisterb, K., & Pischetsrieder, M. (2011). Analysis of nisin A, nisin Z and their degradation products by LCMS/MS. *Food Chemistry*, *127*, 847–854. https://doi.org/10.1016/j.foodchem.2011.01.023

Semedo-Lemsaddek, T., Barreto-Crespo, M. T., & Tenreiro, R. (2012). *Enterococcus* and safety. Nova Science.

Semedo-Lemsaddek, T., Carvalho, L., Tempera, C., Fernandes, M. H., Fernandes, M. J., Elias, M., Barreto, A. S., & Fraqueza, M. J. (2016). Characterization and technological features of autochthonous coagulase-negative staphylococci as potential starters for Portuguese dry fermented sausages. *Journal of Food Science*, *81*(5), 1197-1202. https://doi.org/10.1111/1750-3841.13311

Settanni, L., & Moschetti, G. (2010). Non-starter lactic acid bacteria used to improve cheese quality and provide health benefits. *Food Microbiology*, *27*(6), 691–697. https://doi.org/10.1016/j.fm.2010.05.023

Sharma, A., Kaur, J., Lee, S., & Park, Y. S. (2018). Genetic diversity analysis of *Leuconostoc mesenteroides* from Korean vegetables and food products by multilocus sequence typing. *Applied Microbiology and Biotechnology*, *102*(11), 4853–4861. https://doi.org/10.1007/s00253-018-8942-4

Sharma, A., Lee, S., & Park, Y. S. (2020). Molecular typing tools for identifying and characterizing lactic acid bacteria: a review. *Food Science and Biotechnology*, *29*(10), 1301–1318. https://doi.org/10.1007/s10068-020-00802-x

Shokryazdan, P., Sieo, C. C., Kalavathy, R., Liang, J. B., Alithee, N. B., Jahromi, M. F., & Ho, Y. W. (2014). Probiotic potential of *Lactobacillus* strains with antimicrobial activity against some human pathogenic strains. *BioMed Research International*, *2014*, 1–16. https://doi.org/10.1155/2014/927268

Silva, C. C. G., Silva, S. P. M., & Ribeiro, S. C. (2018). Application of bacteriocins and protective cultures in dairy food preservation. *Frontiers in Microbiology*, *9*, 594. https://doi.org/10.3389/fmicb.2018.00594

Silva, L. F., Sunakozawa, T. N., Amaral, D., Casella, T., Nogueira, M., De Dea Lindner, J., Bottari, B., Gatti, M., & Penna, A. (2020). Safety and technological application of autochthonous *Streptococcus thermophilus* cultures in the buffalo Mozzarella cheese. *Food Microbiology*, *87*, 103383. https://doi.org/10.1016/j.fm.2019.103383

Simha, B. V., Sood, S., Kumariya, R., & Garsa, A. K. (2012). Simple and rapid purification of pediocin PA-1 from *Pediococcus pentosaceous* NCDC 273 suitable for industrial application. *Microbiological Research*, *167*, 544–549. https://doi.org/10.1016/j.micres.2012.01.001

Smid, E. J., & Kleerebezem, M. (2014). Production of aroma compounds in lactic fermentations. *Annual Review of Food Science and Technology, 5*(1), 313-326. https://doi.org/10.1146/annurev-food-030713-092339

Solieri, L., Bianchi, A., Mottolese, G., Lemmetti, F., & Giudici, P. (2014). Tailoring the probiotic potential of non-starter *Lactobacillus* strains from ripened Parmigiano Reggiano cheese by *in vitro* screening and principal component analysis. *Food Microbiology*, *38*, 240–249. https://doi.org/10.1016/j.fm.2013.10.003

Song, D., Ibrahim, S., & Hayek, S. (2012). Recent application of probiotics in food and agricultural science. In E. C. Rigobelo (Ed.), *Probiotics* (pp.4-36). InTech Open, London, UK.

Songisepp, E., Hutt, P., Ratsep, M., Shkut, E., Koljalg, S., Truusalu, K., Stsepetova, J., Smidt, I., Kolk, H., Zagura, M., & Mikelsaar, M. (2012). Safety of a probiotic cheese containing *Lactobacillus plantarum* Tensia according to a variety of health indices in different age groups. *Journal of Dairy Science*, *95*(10), 5495–509. https://doi.org/10.3168/jds.2011-4756

Sornsenee, P., Singkhamanan, K., Sangkhathat, S., Saengsuwan, P., & Romyasamit, C. (2021). Probiotic properties of *Lactobacillus* species isolated from fermented palm sap in Thailand. *Probiotics and Antimicrobial Proteins*, https://doi.org/10.1007/s12602-021-09754-y

Stefanović, E., & McAuliffe, O. (2018). Comparative genomic and metabolic analysis of three *Lactobacillus paracasei* cheese isolates reveals considerable genomic differences in strains from the same niche. *BMC Genomics*, *19*(1), 205. https://doi.org/10.1186/s12864-018-4586-0

Suárez, N., Weckx, S., Minahk, C., Hebert, E. M., & Saavedra, L. (2020). Metagenomics-based approach for studying and selecting bioprotective strains from the bacterial community of artisanal cheeses. *International Journal of Food Microbiology*, *335*, 108894. https://doi.org/10.1016/j.ijfoodmicro.2020.108894

Surachat, K., Sangket, U., Deachamag, P., & Chotigeat, W. (2017) *In silico* analysis of protein toxin and bacteriocins from *Lactobacillus paracasei* SD1 genome and available online databases. *PLoS ONE 12*(8): e0183548. https://doi.org/10.1371/journal.pone.0183548

Suvorov, A. (2020). What is wrong with enterococcal probiotics? *Probiotics and Antimicrobial Proteins*, *12*, 1-4. https://doi.org/10.1007/s12602-020-09633-y

Syrokou, M. K., Themeli, C., Paramithiotis, S., Mataragas, M., Bosnea, L., Argyri, A. A., Chorianopoulos, N. G., Skandamis, P. N., & Drosinos, E. H. (2020). Microbial ecology of Greek wheat sourdoughs, identified by a culture-dependent and a culture-independent approach. *Foods* (Basel, Switzerland), *9*(11), 1603. https://doi.org/10.3390/foods9111603

Taranu, I., Marin, D. E., Braicu, C., Pistol, G. C., Sorescu, I., Pruteanu, L. L., Berindan Neagoe, I., & Vodnar, D. C. (2018). *In vitro* transcriptome response to a mixture of lactobacilli strains in intestinal porcine epithelial cell line. *International Journal of Molecular Sciences*, *19*(7), 1923. https://doi.org/10.3390/ijms19071923

Thierry, A., Pogačic, T., Weber, M., & Lortal, S. (2015). Production of flavor compounds by lactic acid bacteria in fermented foods. In F. Mozzi, R. R. Raya, & G. M. Vignolo (Eds.), *Biotechnology of lactic acid bacteria: Novel applications* (Second Edition ed., pp. 314-340).

Thumu, S. C. R., & Halami, P. M. (2019). Conjugal transfer of *erm*(B) and multiple *tet* genes from *Lactobacillus* spp. to bacterial pathogens in animal gut, *in vitro* and during food fermentation. *Food Research International, 116*, 1066-1075. https://doi.org/10.1016/j.foodres.2018.09.046

Todorov, S. D., Stojanovski, S., Iliev, I., Moncheva, P., Nero, L. A., & Vitanova Ivanovaa, I. (2017). Technology and safety assessment for lactic acid bacteria isolated from traditional Bulgarian fermented meat product "lukanka". *Brazilian Journal of Microbiology*, *48*(3), 576-586. https://doi.org/10.1016/j.bjm.2017.02.005

Tóth, G. A., Csabai, I., Judge, M. F., Maróti, G., Becsei, Á., Spisák, S., & Solymosi, N. (2021). Mobile antimicrobial resistance genes in probiotics. *Antibiotics*, *10*, 1287. https://doi.org/10.3390/antibiotics10111287

Touret, T., Oliveira, M., & Semedo-Lemsaddek, T. (2018). Putative probiotic lactic acid bacteria isolated from sauerkraut fermentations. *PloS One*, *13*(9), e0203501. https://doi.org/10.1371/journal.pone.0203501

Tyson, G. H., Sabo, J. L., Rice-Trujillo, C., Hernandez, J., & McDermott, P. F. (2018). Whole-genome sequencing based characterization of antimicrobial resistance in *Enterococcus*. *Pathogens and Disease*, *76*(2), https://doi.org/10.1093/femspd/fty018

Vesković Moračanin, S., Djukić, D., Zdolec, N., Milijašević, M., & Mašković, P. (2017). Antimicrobial resistance of lactic acid bacteria in fermented food. *Journal of Hygienic Engineering and Design*, *18*, 25–35.

Virdis, C., Sumby, K., Bartowsky, E., & Jiranek, V. (2021). Lactic acid bacteria in wine: technological advances and evaluation of their functional role. *Frontiers in Microbiology*, *11*, 3192. https://doi.org/10.3389/fmicb.2020.612118

Vitorino, L. C., & Bessa, L. A. (2017). Technological microbiology: Development and applications. *Frontiers in Microbiology*, *8*, 827. https://doi.org/10.3389/fmicb.2017.00827

Wang, J., Wang, J., Yang, K., Liu, M., Zhang, J., Wei, X., & Fan, M. (2018) Screening for potential probiotic from spontaneously fermented non-dairy foods based on *in vitro* probiotic and safety properties. *Annals of Microbiology*, *68*, 803–813. https://doi.org/10.1007/s13213-018-1386-3

Wang, Y., She, M., Liu, K., Zhang, Z., & Shuang, Q. (2020). Evaluation of the bacterial diversity of inner Mongolian acidic gruel using Illumina MiSeq and PCR-DGGE. *Current Microbiology, 77*(3), 434–442. https://doi.org/10.1007/s00284-019-01848-9

Waseem, H., Williams, M.R., Stedtfeld, T., Chai, B., Stedtfeld, R., Cole, J., Tiedje, J., & Hashsham, S. (2017). Virulence factor activity relationships (VFARs): a bioinformatics perspective. *Environmental science. Processes & Impacts*, *19*(3), 247-260. https://doi.org/10.1039/c6em00689b

Whaling M. A., Luginaah, I., Reid, G., Hekmat, S., Thind, A., Mwanga, J., & Changalucha, J. (2012). Perceptions about probiotic yogurt for health and nutrition in the context of HIV/AIDS in Mwanza, Tanzania. *Journal of Health, Population and Nutrition*, *30*(1), 31–40. https://doi.org/10.3329/jhpn.v30i1.11273

Yang, C., & Yu, T. (2019). Characterization and transfer of antimicrobial resistance in lactic acid bacteria from fermented dairy products in China. *Journal of Infection in Developing Countries*, *13*(2), 137–148. https://doi.org/10.3855/jidc.10765

Yasir, M., Bibi, F., Hashema, A. M., & Azhar, E. I. (2020). Comparative metagenomics and characterization of antimicrobial resistance genes in pasteurized and homemade fermented Arabian laban. *Food Research International*, *137*, 109639. https://doi.org/10.1016/j.foodres.2020.109639

Yasmin, I., Saeed, M., Khan, W. A., Khaliq, A., Chughtai, M., Iqbal, R., Tehseen, S., Naz, S., Liaqat, A., Mehmood, T., Ahsan, S., & Tanweer, S. (2020). *In vitro* probiotic potential and safety evaluation (hemolytic, cytotoxic activity) of *Bifidobacterium* strains isolated from raw camel milk. *Microorganisms*, *8*(3), 354. https://doi.org/10.3390/microorganisms8030354

Yildirim, Z., Öncül, N., Yildirim, M., and Karabiyikli, Ş. (2016). Application of lactococcin BZ and enterocin KP against *Listeria monocytogenes* in milk as biopreservation agents. *Acta Alimentaria*, *45*, 486–492. https://doi.org/10.1556/066.2016.45.4.4

Yoshii, K., Hosomi, K., Sawane, K., & Kunisawa, J. (2019). Metabolism of dietary and microbial vitamin B family in the regulation of host immunity. *Frontiers in Nutrition*, *6*, 48. https://doi.org/10.3389/fnut.2019.00048

You, I., & Kim, E. B. (2020). Genome-based species-specific primers for rapid identification of six species of *Lactobacillus acidophilus* group using multiplex PCR. *PloS One, 15*(3), e0230550. https://doi.org/10.1371/journal.pone.0230550

Yu, D., Shi, K., Wen, X., Xie, F., Wang, T., Liu, S., & He, L. (2018). Evidence of the genetic diversity and clonal population structure of *Oenococcus oeni* strains isolated from different wine-making regions of China. *Journal of Microbiology* (Seoul, Korea), *56*(8), 556–564. https://doi.org/10.1007/s12275-018-7568-7

Yvon, M. M. (2006). Key enzymes for flavour formation by lactic acid bacteria. *Australian Journal of Dairy Technology, 61*(2), 88-96.

Zago, M., Bardelli, T., Rossetti, L., Nazzicari, N., Carminati, D., Galli, A., & Giraffa, G. (2021). Evaluation of bacterial communities of Grana Padano cheese by DNA metabarcoding and DNA fingerprinting analysis. *Food Microbiology*, *93*, 103613. https://doi.org/10.1016/j.fm.2020.103613

Zarzecka, U., Chajęcka-Wierzchowska, W., & Zadernowska, A. (2022). Microorganisms from starter and protective cultures - Occurrence of antibiotic resistance and conjugal transfer of *tet* genes *in vitro* and during food fermentation. *LWT-Food Science and Technology*, *153*, 112490. https://doi.org/10.1016/j.lwt.2021.112490

Zarzecka, U., Zadernowska, A., & Chajacka-Wierzchowska, W. (2020). Starter cultures as a reservoir of antibiotic resistant microorganisms. *LWT-Food Science and Technology*, *127*, 109424. https://doi.org/10.1016/j.lwt.2020.109424

Zhang, Y., Chen, H., & Pan, K. (2017). Nanoencapsulation of food antimicrobial agents and essential oils. In S. M. Jafari (Ed.), Nanoencapsulation of food bioactive ingredients (pp. 183–221). Elsevier. https://doi.org/10.1016/B978-0-12-809740-3.00005-2

Zotta, T., Ricciardi, A., Condelli, N., & Parente, E. (2021). Metataxonomic and metagenomic approaches for the study of undefined strain starters for cheese manufacture. *Critical Reviews in Food Science and Nutrition*, 1–15. https://doi.org/10.1080/10408398.2020.1870927

Žugić Petrović, T., Ilić, P., Grujović, M., Mladenović, K., Kocić-Tanackov, S., & Čomić, Lj. (2020). Assessment of safety aspect and probiotic potential of autochthonous *Enterococcus faecium* strains isolated from spontaneous fermented sausage.

Biotechnology Letters, *42*(8), 1513-1525. https://doi.org/10.1007/s10529-020-02874-5

Žugić Petrović, T., Ilić, P., Muruzović, M., Mladenović, K., Stanisavljević, D., & Čomić, Lj. (2019). Dry-fermented sausage as probiotic carrier food. *Fleischwirtschaft*, *99*(2), 100–103.

Table 1. A plethora of molecular tools and corresponding features

	Methodology	**Discriminatory power**	**Repeatability /reproducibility**	**Data analysis /interpretation**	**Duration (days)**	**Associated cost**	**Recent applications (last 5 years)**	**References**
PCR-based methodologies	AFLPs	High	High	Difficult	2	high	*Lacticaseibacillus casei* group; *Oenococcus* spp.	Jarocki et al., (2020); Yu et al., (2018)
	AP-PCR/RAPDs	High	Median	Moderate	1	low to median	*Apilactobacillus kunkeei, Enterococcus* spp. *Fructobacillus fructosus Lactiplantibacillus plantarum, L. fermentum, L. casei, L. delbrueckii subsp. lactis* and *L. pentosus, Lactococcus lactis* ssp., *Leuconostoc mesenteroides, L. brevis*	Biolcati et al., (2020); Bindu & Lakshmidevi, (2021); De Pasquale et al., (2019); Pérez-Díaz et al., (2021); Syrokou et al., (2020)
	DGGE/TGGE	Variable	Median	Difficult	>3	high	*Apilactobacillus kunkeei, F. fructosus, L. sanfranciscensis, Lactiplantibacillus plantarum, L. delbrueckii subsp. lactis, Lactobacillus amylolyticus, L. alimentarius, L. hamsteri, L. helveticus, L. panis, L. plantarum, L. pontis, Leuconostoc lactis, Levilactobacillus brevis, Limosilactobacillus fermentum*	Comasio et al., (2020); Díaz-Muñoz et al., (2021); Iorizzo et al., (2020); Figueroa-Hernández et al., (2019); Syrokou et al., (2020); Wang et al., (2020)
	Genus/species specific PCR	Variable	High	easy	1	low to median	*Enterococcus* spp., Lactic acid bacteria, *L. acidophilus* group, *L. casei* group, *Lactobacillus sakei* group, *L. plantarum,* Lactococcus *spp.* *Lactiplantibacillus plantarum,* *Leuconostoc* spp. *Pediococcus* spp., *Oenococcus sicerae*	Biolcati et al., (2020); Chaikaew et al., (2017); Cousin et al., (2019a; 2019b); Fusco et al., (2019); Huang et al., (2018); Jarocki et al., (2020); Park et al., (2017); Syrokou et al., (2020); Touret et al., (2018); You et al., (2020)
	MLST/cgMLST/wgMLST	High	High	Difficult	>3	high	*Enterococcus faecalis, L. plantarum, Lactobacillus pentosus, Lactococcus lactis,* *Leuconostoc mesenteroides*	Chen et al., (2021); Lee et al., (2017); Luiz et al., (2016); Neumann et al., (2019); Pérez-Díaz et al., (2021); Sharma et al., (2018)
	PCR-RFLPS	Median	High	easy to moderate	1	low to median	*Lactobacillus casei* group	Jarocki et al., (2020); López-Seijas et al., (2020)
	qRT-PCR	High	High	Moderate	1	high	Lactic acid bacteria; *Lactobacillus casei* group	Jarocki et al., (2020); Kim et al., (2020); Martins et al., (2020); Silva et al., (2020)
	WGS	High	High	Difficult	>3	high	*Enterococcus spp., L. plantarum, Lactobacillus buchneri*	Nethery et al., (2019); Mannaa et al., (2019); Rodrigo-Torres et al., (2019); Tyson et al., (2018)

	First generation "Sanger" sequencing	High	High	Difficult	>3	high	Lactic acid bacteria, *Enterococcus spp., Lactobacillus spp., Pediococcus* spp.	Jafari-Nasab et al., (2021); Kadri et al., (2021); Motey et al., (2021); Pradhan et al., (2019); Sornsenee et al., (2021)
	Second/Third generation sequencing Targeted/non-targeted metagenomics	High	High	Difficult	>3	High	Cheese Fermented meat sausages Kefir Kimchi Palm Wine Pickled cowpea Sourdoughs	Astudillo-Melgar et al., (2019); Comasio et al., (2020); Cruxen et al., (2019); Ferrocino, (2018); Franciosa et al., (2018); Guo et al., (2021); Kazou et al., (2021); Kim et al., (2021); Suárez et al., (2020); Zago et al., (2021); Zotta et al., (2021)
Non PCR-based methodologies	Maldi-TOF	High	High	Difficult	1	High	*E. faecalis,* Lactic acid bacteria, *Lactobacillus casei* group, *Lactobacillus curvatus, L. diolivorans, L. paracasei, L. plantarum, L. rhamnosus, Lactococcus lactis, L. mesenteroides*	Baccouri et al., (2019); Gantzias et al., (2020); Jarocki et al., (2020); Sánchez-Juanes et al., (2020)
	Microarrays	High	High	difficult	<3	High	*L. rhamnosus, L. plantarum,* and *L. paracasei* *Lactobacillus* spp.	Endo et al., (2020); Taranu et al., (2018)
	PFGE	High	High	moderate	>3	High	*Enterococcus* spp., Lactic acid bacteria, *L. paracasei, Lactococcus lactis*	Luiz et al., (2016); Russo et al., (2018); Stefanović & McAuliffe (2018); Yang & Yu, (2019)
	RFLPs	low to median	median to high	moderate	1 to 3	median	Lactic acid bacteria	Chen et al., (2017); Hajigholizadeh et al., (2020); Penido et al., (2018)

Table 2. Classification, description, and mechanism of action of bacteriocins

Class of bacteriocins and properties		Subclass	Description	Examples	Producer	Target microorganism	References	Mechanism of action
Class I: The Lantibiotics – bacteriocins are post-translationally modified, linear or globular peptides containing lanthionine, β-methyl lanthionine and dehydrated amino acids; 19-28 amino acids (<5 kDa)	Ia: Lantibiotics	I	elongated, screw shaped, positively charged, amphipathic, flexible molecules; molecular mass varies between 2 to 4 kDa	Nisin A/Z	*Lactococcus lactis*	*L. monocytogenes*, *S. aureus*, *C. tyrobutyricum* and other LAB	Fraqueza et al., (2016); Laranjo et al., (2017)	act through pore formation, through membrane depolarization, of the cytoplasmic membrane of the sensitive target species
				Pep5	*Staphylococcus epidermidis*	*S. aureus, Staphylococcus spp.*	Newstead et al., (2020); Fontana et al., (2006)	
				Subtilin	*Bacillus subtilis*	*B. amyloliquefaciens, L. lactis, L. plantarum, S. aureus* and *E. faecalis*	Qin et al., (2019)	
		II	globular in structure and interfere with cellular enzymatic reactions; molecular mass lies between 2 to 3 kDa	Lactocin S	*Lactobacillus sakei* L45	*L. monocytogenes*	Quinto et al., (2016)	
				Lacticin 3147	*Lactococcus lactis* subsp. *lactis*	*L. monocytogenes*	Ribeiro et al., (2016); Yildirim et al., (2016)	
		III	lantibiotic-like peptides grouped based on affinity of modifying enzymes, which have not been shown to have antimicrobial activity	Siamycin-I Aborycin	*Streptomyces* spp.	*E. faecalis* 5	Nakayama et al., (2007)	
				Natamycin	*Streptomyces natalensis*	Moulds and yeasts	Zhang et al., (2017)	
	Ib: Labyrintopeptins	/	presence of labionin, a previously unidentified carbocyclic, posttranslationally modified amino acid	Labyrinthopeptin A1	*Actinomadura namibiensis* DSM 6313	Viruses (anti-HIV and anti-HSV activity)	Ferir et al., (2013)	
				Mersacidin	*Bacillus* sp. strain HIL Y-85,54728	*Propionibacterium acnes*	Kashyap, (2019)	
	Ic: Saktibiotics	/	cyclic peptide, smaller in size and unusually posttranslationally modified, with bonds formed between sulphur from three cysteine residues and α-carbon from two phenylalanines and one threonine	Subtilozin A	*Bacillus subtilis*	*Bacillus cereus, L. monocytogenes, M. luteus*, and *S. aureus*	Khochamit et al., (2015)	
				Thuricin CD	*Bacillus thuringiensis* SF361	*Clostridium difficile*	Rea et al., (2010)	
Class II: The Non-Lantibiotics – heat stable, non-modified, cationic, hydrophobic peptides; contain a double–glycine	IIa: Pediocin-like peptides	/	pediocin-like or listeria active bacteriocins subclass possesses an N-terminal consensus sequence Tyr-Gly-Asn-Gly-Val-Xaa-Cys	Pediocin PA-1	*P. acidilactici* PAC1.0	*L. monocytogenes*, *Enterococcus* spp. and other LAB	Fraqueza et al., (2016); Laranjo et al., (2017)	induce increased membrane permeability by the formation of pores which leads to disruption of the membrane potential,
				Leucocin A	*Leuconostoc geldium* UAL 187	*L. monocytogenes, Enterococcus* spp., *Carnobacterium* spp., lactobacilli,	Etayash et al., (2014); Makhloufi et al., (2013)	

leader peptide; pediocin-like peptides; <10 kDa						*Leuconostoc* spp, *Pediococcus* spp., *Clostridium* spp. and are inactive toward gram-negative bacteria		and leads to the emptying of the internal ATP depots of the target cell
				Mesentericin Y105	*Leuconostoc mesenteroides* Y105	herpes simplex virus, *E. faecalis, L. monocytogenes*	Morisset et al., (2004)	
				Enterocin NKR-5-3C	*Enterococcus faecium* NKR-5-3	*L. monocytogenes*	Khan et al., (2010); Yildirim et al., (2016)	
				Plantaricin	*Lactiplantibacillus plantarum*	*L. monocytogenes, S. aureus, C. perfringens, C. tyrobutyricum, B. cereus, Enterococcus* spp., *B. thermosphacta, Salmonella* spp., *Pseudomonas* spp., *E. coli,* and other LAB	Fraqueza et al., (2016); Laranjo et al., (2017)	
				Curvacin A	*Lactobacillus curvatus*	*L. monocytogenes, S. aureus*, *B. thermosphacta*, *Pseudomonas* spp.*, E. coli* and other LAB	Fraqueza et al., (2016); Laranjo et al., (2017)	
				sakacin G sakacin P	*Lactobacillus sakei*	*L. monocytogenes*, *S. aureus*, *Enterococcus* spp., *Brochothrix thermosphacta*, *Pseudomonas* spp., *Campylobacter* spp., *E. coli*, *Klebsiella* spp., and other species of LAB	Fraqueza et al., (2016); Laranjo et al., (2017)	
	IIb: Two-peptides	/	require synergy of two complementary peptides; mostly at ionic peptides; form ß-pleated plates rather than α-helices	Lactacin F	*Lactobacillus acidophilus*	*Salmonella enteritidis, E. coli, P. aeruginosa*, and *S. aureus*	*Barefoot et al., (1994)*	
				Enterocin NKR-5-3AZ	*Enterococcus faecium*	*L. monocytogenes*	Khan et al., (2010); Yildirim et al., (2016)	
				Gassericin T	*Lactobacillus gasseri LA327*	in combination with glycine inhibits *B. cereus*	Arakawa et al., (2009)	
	IIc: Circular	/	circular cationic peptides, thermostable, not subject to proteolytic degradation and show antilisterial activity	Lactococcin B	*Lactococcus lactis* subsp. *cremoris* 9 B4	*L. monocytogenes*	Ribeiro et al., (2016); Yildirim et al., (2016)	
				Enterocin B	*Enterococcus faecium* T136	*S. aureus, Acinetobacter baumannii, L.*	Ankaiah et al., (2018)	

						monocytogenes and *E. coli*		
				Uberolysin A	*Streptococcus uberis*	*S. aureus, E. coli, E. faecalis* and *Corynebacterium* spp.	Lasagno et al., (2019)	
	IId: Non-pediocin-like linear	/	linear bacteriocins non-pediocin like, single peptide	Lacticin Q	*Lactococcus lactis* QU 5	*L. monocytogenes*	Ribeiro et al., (2016); Yildirim et al., (2016)	
				Leucocin B	*Leuconostoc pseudomesenteroides* QU 15	*E. faecium, L. sakei subsp. sakei, L. mesenteroides, Listeria innocua, Listeria ivanovii subsp. ivanovii L. monocytogenes, S. pneumoniae*	Makhloufi et al., (2013)	
Class III: Bacteriocins – heat-labile; large molecular mass peptides; >30 kDa	IIIa: Bacteriolytic	/	Bacteriolytic; shows a domain structure in which different domains are responsible for translocation, receptor binding and inhibitory activity	Lysostaphin	*Staphylococcus simulans* subsp. *Staphylolyticus*	*S. aureus, S. carnosus, S. epidermidis, S. haemolyticus*	Bastos et al., (2010)	catalyse the hydrolysis of cell wall resulting in cell lysis
	IIIb: Non-bacteriolytic	/	non-lytic proteins, sensitive to proteolytic enzymes and to high temperature	Helveticin J	*Lactobacillus helveticus* 481	*L. bulgaricus*	Joerger & Klaenhammer, (1986)	disturb the glucose uptake by cells, starving them and disturbs the membrane potential
				Caseicin 80	*Lacticaseibacillus casei*	Another lactobacili strains	Rammelsberc & Radler, (1990)	

Table 3. Bacteriocins used for commercial purposes

Bacteriocin	Commercial name	Application	Target microorganisms	References
Nisin A	Nisaplin® Danisco	Dairy, culinary, meat, bakery products and beverages	*Listeria* spp., *Bacillus* spp., *Clostridium* spp.	Abriouel et al., (2011); Grande et al., (2014)
Nisin A, Nisin Z	Nisin A® Nisin Z®	Dairy products, bakery, beverages, delicacies, meat	*Listeria* spp., *Clostridium* spp., *Bacillus cereus*	Dicks et al., (2011); Schneidera et al., (2011)
Nisin	Chrisin®	Meat, sausages, and spore-forming bacteria in cheese	*Clostridium botulinum*, *Listeria monocytogenes*	Aymerich et al., (2008)
Natamycin	Natamax®	Cheese, fresh dairy products, processed meat, and beverages	Yeasts and moulds	Pintado et al., (2010)
Pediocin	ALTA® 2351 2341	Meat products	*Listeria monocytogenes*	Abriouel et al., (2011)
Pediocin	Fargo 23®	Meat products	*Listeria monocytogenes*	Aymerich et al., (2008)
Pediocin PA1	Microgard™	Meat products	*Listeria monocytogenes*	Simha et al., (2012)
Pediocin, sakacin	Bactoferm FLC®	Meat products	*Listeria monocytogenes*	Jofré et al., (2008); Abriouel et al., (2011);

Table 4. Lactic acid bacteria, fermentations and resulting aroma and taste compounds

Lactic acid bacteria	Foods	Processes/Enzymes	Flavour Compounds (Aroma/Taste)	References
Lactococcus chungangensis	dairy products	lipolysis/lipases	methylketones secondary alcohols esters lactones	Konkit & Kim, (2016)
Lactobacillus spp.		proteolysis/proteinases Amylases		
Lactobacillus spp.	meat products	Maillard reaction-Strecker degradation	pyrroles pyrazines oxazoles thiophenes thiazoles	Flores, (2018); Flores & Toldrá, (2011); Laranjo et al., (2017); Laranjo et al., (2019)
		lipid oxidation	aldehydes ketones alcohols aliphatic hydrocarbons acids esters	
Lactiplantibacillus plantarum	table olives	alcoholic and heterolactic fermentations	methanol ethanol acetic acid other alcohols esters	Hurtado et al., (2012)
Leuconostoc mesenteroides *Lactiplantibacillus plantarum* *Levilactobacillus brevis*	Sauerkraut		lactate acetate ethanol carbon dioxide	Marco et al., (2017); Touret et al., (2018)
Leuconostoc mesenteroides *Lactiplantibacillus plantarum*	pickles	homolactic and heterolactic fermentations	lactic acid acetic acid ethanol	Mao & Yan, (2019)
Oenococcus oeni *Lactobacillus* spp.	Wine	sugar breakdown		Cappello, Zapparoli, Logrieco, & Bartowsky, (2017)
Lactobacillus spp.	Beer	sugar breakdown		Dysvik et al., (2020)
Lacticaseibacillus casei and Lactiplantibacillus plantarum	Kombucha	sugar breakdown		Nguyen et al., (2015)
Lactiplantibacillus plantarum *Limosilactobacillus fermentum*	Cocoa	sugar breakdown	organic acids (e.g. lactic acid)	Ho et al., (2018)

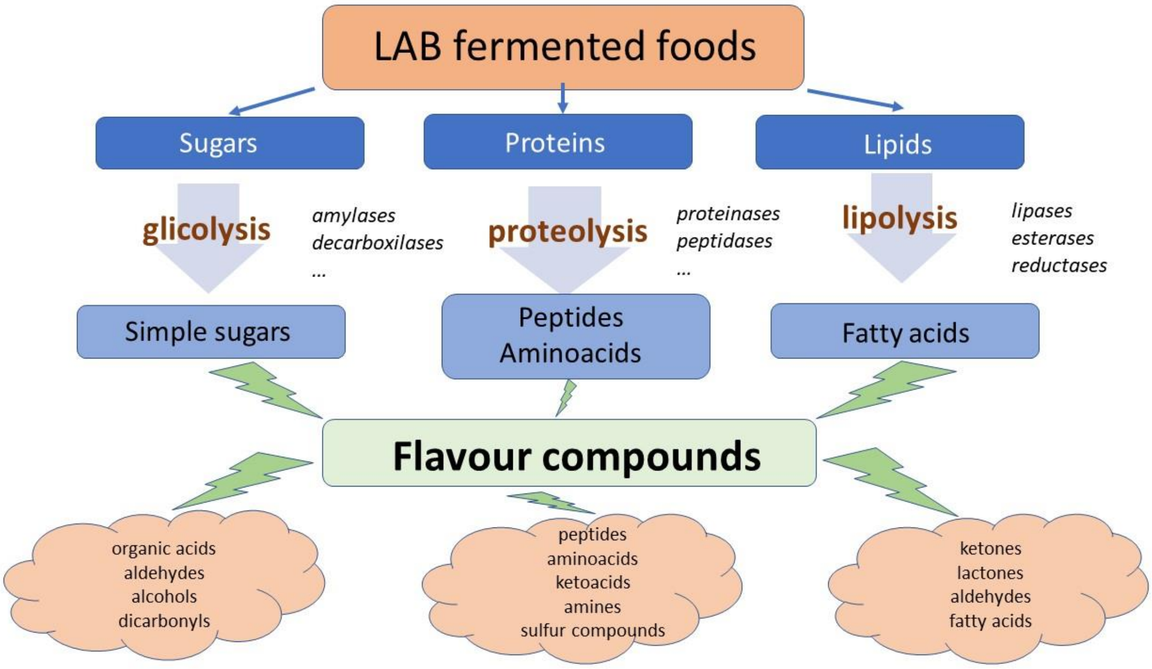

Figure 1. Microbial metabolic pathways leading to the generation of flavour in nsLAB fermented foods