



Invited review: Review of taxonomic changes in dairy-related lactobacilli

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ABSTRACT

The genus *Lactobacillus* has represented an extremely large and diverse collection of bacteria that populate a wide range of habitats, and which may have industrial applications. Researchers have grappled with the immense genetic, metabolic, and ecological diversity within the genus *Lactobacillus* for many years. As a result, the taxonomy of lactobacilli has been extensively revised, incorporating new genus names for many lactobacilli based on their characteristics including genomic similarities. As a result, many lactobacilli traditionally associated with dairy products now have new genus names and are grouped into new clades or clusters of species. In this review, we examine how the taxonomic restructuring of the genus *Lactobacillus* will affect the dairy industry and discuss lactobacilli associated with dairy production, processing, and those that confer possible health benefits when delivered by dairy products. **Key words:** *Lactobacillus*, dairy products, cheese, taxonomy

INTRODUCTION

What is in a name? Taxonomy is the science of systematically classifying organisms into a hierarchy (domain, phylum, class, order, family, genus, species, subspecies) based on characteristics that indicate relatedness. Taxonomically, organisms more closely related share more genetic similarities, and, hence, more phenotypic traits in common. Biologists use taxonomy as the basis for nomenclature, or naming of organisms. Biological nomenclature is important so that there can be common and consistent communication about living organisms for scientific research or medical and industrial applications (Parker et al., 2019).

For microorganisms, taxonomic classification can be difficult because they lack many obvious distinguish-

ing features, and due to horizontal gene transfer, distantly related organisms may share similar physiologic characteristics. New genetic methods, especially whole genome sequencing, provide more precise metrics for defining microbial taxonomy. This allows researchers to capture an organism's physiological, ecological, and evolutionary relationship more accurately. The genus name *Lactobacillus* has represented an extremely large and diverse collection of microorganisms that inhabit a wide range of habitats, and many may have industrial and medical applications. Because of the genetic and ecological diversity within the genus *Lactobacillus*, Zheng et al. (2020) have recently reevaluated the genus and provided new genus names that group organisms into new clades or clusters of species. This includes the lactobacilli that are common in dairy foods and products. The purpose of this review is to help dairy producers and dairy researchers who do not have a strong microbiology understand the taxonomic restructuring of the *Lactobacillus* genus. The organisms discussed are primarily the lactobacilli associated with dairy production, processing, and those that confer possible health benefits when delivered by dairy products.

INITIAL LACTOBACILLUS TAXONOMY

Researchers have been grappling with the immense genetic, metabolic, and ecological diversity within the genus *Lactobacillus* for many years (Vandamme et al., 1996; Felis and Dellaglio, 2007; Salvetti et al., 2012; Mattarelli et al., 2014; Zheng et al., 2015; Sun et al., 2015; Wittouck et al., 2019a,b; Zheng et al., 2020). Lactobacilli were some of the earliest bacteria described due, in part, to their presence in the microbiota of fermented milks and their reported health benefits to consumers (Tannock, 2004). Initially, taxonomy of microorganisms (bacteria) was based on their physical characteristics (gram stain, cell morphology, colony appearance) and on their growth parameters such as optimum incubation temperature, pH tolerance, and oxygen requirements. Methods based on specific composition of cell components were also used to differ-

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entiate lactobacilli including cell wall (peptidoglycan) composition and membrane fatty acid profiles (Davis, 1964). These classifications are only as accurate as the databases used for comparison and, in the case of cell membrane composition, also dependent on the growth media because it can influence fatty acid composition.

Biochemical characterization, determining substrates utilized and the metabolic end products produced, generated a phenotype-based taxonomy for lactobacilli. This was used to divide lactobacilli into 3 general groups based on their fermentative ability; obligate homofermenters, facultative heterofermenters, and obligate heterofermenters (Hammes and Vogel, 1995). These designations (classifications) were based on lactobacilli either having or lacking key enzymes in several fermentation pathways. Obligate homofermenters use the Embden-Meyerhof pathway to convert glucose to lactic acid, but cannot use the pentose phosphate pathway to ferment pentoses. Obligate heterofermenters exclusively use the pentose phosphate pathway, whereas facultative heterofermenters using the Embden-Meyerhof pathway but also ferment pentoses. This classification proved very useful in dairy production because lactobacilli from each category play significant roles in dairy processing and product quality.

In the 1980s, bacterial taxonomy entered the genetic age with the use of DNA sequencing to determine the 16S rRNA gene base sequence. Comparison of 16S rRNA gene base sequences allowed the generation of a true phylogenetic tree for taxonomy, which graphed the relatedness of lactobacilli based on divergence from common ancestors. It quickly became the gold standard for determining the place of an organism on the taxonomic tree and gave accurate genus and species designations because metabolic properties among lactobacilli were more variable than initially thought (Williams et al., 2000; Clarridge, 2004).

Revised Taxonomy for *Lactobacillus*

Development of whole genome sequencing, and the computational capacity to rapidly compare entire bacterial genomes, dramatically advanced bacterial taxonomy. Recent studies utilizing this approach, culminating in Zheng et al. (2020), proposed using a variety of genomics metrics for classifying organisms within the *Lactobacillus* genus and argued for a revision to its taxonomy (Mattarelli et al., 2014; Sun et al., 2015; Salvetti et al., 2018; Wittouck et al., 2019b; Zheng et al., 2020). The ability to sequence an organism's genome and to compare the sequence of key conserved proteins between genomes has allowed restructuring of *Lactobacillus* taxonomy and the clarification of taxonomic relationships based on genetic, physiological, and

ecological characteristics. Although original *Lactobacillus* taxonomies were based on their ability to ferment specific hexoses, that classification has been superseded by genomic analysis which showed that metabolic capabilities were not sufficient for representing the diversity or evolutionary history of this group. Species within this taxon share only a small number of core genes, whereas the pan genome (the entire collection of genes within the genus) of the *Lactobacillus* genus complex is very large (Broadbent et al., 2012; Sun et al., 2015; Wittouck et al., 2019b). This diversity is attributed to adaptations to diverse environments and horizontal gene transfer events through mobile elements and bacteriophage (Sun et al., 2015; Stefanovic, et al., 2017b; Duar et al., 2017).

The amount of genetic diversity calculated based on total nucleotide identity, average nucleotide identity, GC content, genome size, and pan genome comparisons support the conclusion that diversity within the former genus *Lactobacillus* was at least equivalent to that seen within biological families (Sun et al., 2015; Zheng et al., 2015). Further, the former genus *Lactobacillus* is paraphyletic with the family *Leuconostocaceae* and genus *Pediococcus*, indicating evolutionary relationships within these taxa were not adequately resolved and that a revised taxonomy was necessary to meet the standard expectations for defined genera (Sun et al., 2015; Salvetti et al., 2018; Pot et al., 2019). Recently, an analysis of over 2,400 *Lactobacillus* genomes examined *Lactobacillus* taxonomy using a 6% difference for speciation to suggest restructuring the taxonomy into 239 de novo species and 8 new species (Wittouck et al., 2019a,b). The number of *Lactobacillus* species, which exceeded 260 (Table 1), has proven cumbersome with some species in groups not representative of their metabolic characteristics, natural environment, or common genetic sequences. Modern sequencing technology and bioinformatic analysis, combined with new information about physiology, habitat, and lifestyle, have made a more robust classification of the lactobacilli possible (Pot et al., 2019).

Zheng et al. (2020) used a polyphasic approach to characterize 261 described species of *Lactobacillus*,

Table 1. Number of lactobacilli species over time

Year	Number of species	Reference
1995	67	Hammes and Vogel, 1995
2003	80	Satokari et al., 2003
2007	106	Felis and Dellaglio, 2007
2012	152	Salvetti et al., 2012
2015	213	Sun et al., 2015
2020	261	Zheng et al., 2020

Pediococcus, and *Leuconostocaceae*. A polyphasic approach involves comparisons of genomic analysis, phenotypic characteristics, and ecological habitats. Genetic metrics used included average nucleotide identity, average AA identity, core-gene AA identity, and conserved genes. This analysis divided the genus *Lactobacillus* into 26 lineages with 23 new genera, which captured the evolutionary lineage of *Lactobacillaceae*, and can serve as a useful and practical taxonomy (Zheng et al., 2020).

Several metabolic and genetic trends become more apparent in the updated taxonomy. The heterofermentative and homofermentative species of lactobacilli generally separate into 2 large groups within the family *Lactobacillaceae*. The terms obligate and facultative are no longer used in the description of fermentation. The new definition of homofermentative organisms is those that metabolize hexoses using the Embden-Meyerhoff pathway to pyruvate, and heterofermentative organisms are those that metabolize hexoses using the phosphoketolase pathway to pyruvate and acetyl-phosphate. Pentose metabolism is still considered variable across the new taxonomic groups at the species and strain level and is not used as a defining feature. Within each group, other characteristics are also consistent within the phylogenomic classification and proposed genera, including metabolic similarities, signature genes, and similar habitats (Zheng et al., 2015; Duar et al., 2017; Salvetti et al., 2018; Wittouck et al., 2019a; Zheng et al., 2020). For example, lactobacilli symbiotic with humans or mammals have a decreased genome size, but retain a large carbohydrate range, presumably as an adaptation to diets containing diverse substrates. These symbionts may also show acid or bile resistance (Zheng et al., 2015; Duar et al., 2017). In comparison, most lactobacilli involved with food fermentations, including dairy, have larger genomes that may provide habitat flexibility and are considered either free-living or nomadic, meaning they are found in diverse habitats or have a prime habitat that has not been identified (Stefanovic et al., 2017a; Duar et al., 2017).

Lactobacilli used in food fermentations do not cluster in distinct genera in the new taxonomy, but instead are found throughout the *Lactobacillaceae* suggesting that they have a free-living ancestor associated with either animals or plants (Stefanovic et al., 2017b). Most members of *Paucilactobacillus* for example, have been isolated from silage or plant-related environments, but they have also been found in dairy products, sometimes as defect-causing contaminants (Oberg et al., 2016). Other physiological traits that appear to cluster in phylogroups and that may have applications to dairy include acid resistance, bacteriocin production, bacteriophage resistance, carbohydrate use patterns, lactate

metabolism, and amino acid metabolism pathways (Zheng et al., 2015, 2020).

Need for Reclassification in the Dairy Industry

The economic applications of the *Lactobacillaceae* in food, probiotic, industrial, and medical applications complicate the argument for reclassification because the genus name *Lactobacillus* is ubiquitous and familiar. However, reclassification is important because the applications of lactobacilli in industry depends on the use of species or strains with the desired metabolic capabilities and growth parameters (Stefanovic et al., 2017a; Duar et al., 2017; Pot et al., 2019). The phylogenomic taxonomy developed by Zheng et al. (2020) is largely consistent with metabolic capabilities, lifestyle strategies, and habitats. The new taxonomy will be of greater value for industrial and medical applications (Duar et al., 2017; Zheng et al., 2020), because it will be easier to identify specific organisms that have the desired metabolic pathways, products, and growth conditions required for commercial or medical production.

This is especially important in dairy because an organism's ability to produce a desired product requires strictly defined, and reproducible, growth parameters such as the types and amount of sugars, fermentation temperatures, and presence of other organisms. Even within the dairy industry, lactobacilli occur in diverse habitats or ecosystems and have a wide variety of roles and effects (Stefanovic et al., 2017a). The reclassification by Zheng et al. (2020) allows improved communication among scientists, industries, regulators, and the public about the specific capabilities of each species (Pot et al., 2019). It will also allow for greater consistency and reproducibility, especially in the food industry, and potentially can be used to identify genes for creating designer lactobacilli that precisely deliver a desired product (Pot et al., 2019). A higher resolution framework based on physiological and ecological characteristics, in addition to genomic similarities, will help those in industry identify organisms more likely to meet application demands, produce desired products, or identify ways for controlling unwanted organisms without inhibiting those that have desired capabilities.

The taxonomic revision will require dramatic and potentially expensive changes for the scientific community, companies, governments, and, even, consumers. Long-term stability of the new nomenclature is of the utmost importance, so that newly identified organisms can be absorbed into the taxonomy in a meaningful way. This is especially important as new organisms are now being discovered, often without cultured representatives, through Next Generation Sequencing of

complex environments such as the microbiome of the gut (Pot et al., 2019).

Revision of *Lactobacillus* nomenclature is not without concern or controversy. Reclassification may initially cause problems because of regulatory, safety, or legal complications and misunderstandings (Salveti et al., 2018; Pot et al., 2019; Wittouck et al., 2019b). A stable nomenclature is necessary for clear communication between stakeholders. Commercial and legal effects of the taxonomic change include patent applications and enforcement, ingredient lists, import and export certifications, marketing, and consumer education (Pot, et al., 2019). Realizing implementation of name changes may take a substantial amount of time, but as noted at a workshop of the Lactic Acid Bacteria Industrial Platform, efforts to communicate the change through an easy-to-use website or cell phone app would help facilitate the change (Pot et al., 2019). Such a website exists at <http://lactobacillus.ualberta.ca/> where old names of *Lactobacillus* species can be entered, and the new genus names and descriptions are provided.

Lactobacilli relevant to the dairy industry have been organized into categories based on relevance to the industry with their original taxonomic name and new taxonomic designation (Table 2). In addition, supplemental material has been added relative to each organism's role in dairy microbiology. If an organism has multiple uses or roles in dairy microbiology, it is grouped with its most significant role and additional roles are added in the description. Tables have been used to assist in finding organisms in functional groupings and for listing the new taxonomic names of lactobacilli with minor connections to the dairy industry. The 16S rRNA gene accession number, genome size including G+C content, genome sequence accession number and the culture repository for each organism described in this review can be found in Zheng et al. (2020). In addition, Zheng et al. (2020) also contains the reference to the original description of each species when it was initially proposed along with the basonym, which is the original proposed species name and the author citation, and the type strain.

LACTOBACILLI AND DAIRY FOODS

Lactic acid bacteria can be divided into 2 groups relative to fermented dairy foods; starter lactic acid bacteria intentionally added to the milk, and nonstarter lactic acid bacteria (NSLAB) that are part of the milk and production facility microbiota which contaminate the milk or product during production. Fermented dairy products can be divided into 2 major groups, liquid or semisolid products where no liquid has been removed, and products where whey has been removed during

manufacture. Liquid and semisolid products include fermented milks and yogurts, whereas cheese manufacture includes a whey-removal step where some water, whey proteins, minerals, and lactose are removed.

In the manufacture of cheese, starter cultures can be added as mixtures of defined or undefined strains purchased from a culture supplier and added directly to milk, or as a bulk starter culture prepared in the factory with the seed culture purchased from a supplier. In some smaller scale artisan operations, the starter culture is propagated in-house by fermentation of whey from the previous day's production run. In such cases, the fermentation is uncontrolled and strain variations likely occur over time (Beresford et al., 2001). The mesophilic *Lactococcus lactis* is the prime acid-producing starter culture for many cheeses. For cheeses that have a higher cooking temperature, thermophilic starter cultures composed of lactobacilli and *Streptococcus thermophilus* are employed and are usually the acid-producing bacteria dominant in self-propagated starter cultures.

The *Lactobacillus* portion of a starter culture (Table 3) helps control the pH of the fermented product, influences growth of other microorganisms, and causes proteolysis and lipolysis, which influences product texture and formation of specific flavor compounds (Lobo di Palma et al., 1987). In addition, lactobacilli help provide biopreservation through production of alcohols, organic acids, carbon dioxide, diacetyl, hydrogen peroxide, and other substances capable of inhibiting growth of unwanted microorganisms (Helander et al., 1997; Ortiz-Rivera et al., 2017).

Nonstarter lactobacilli exert a wide range of effects on fermented dairy products. Some NSLAB are viewed as a positive or desired addition to the cheese microbiota, whereas others are associated with defects such as slits and cracks, off-flavors, and crystal formation in Cheddar cheese (Crow et al., 1995; Broadbent et al., 2003). The NSLAB enter the cheese because they either survive pasteurization or are introduced postpasteurization from the dairy plant environment and often become the predominate bacteria in Cheddar cheese at the time of sale (Oberg et al., 2011).

LACTOBACILLI USED AS STARTER CULTURES

Species Associated with Yogurt and Fermented Milks

Yogurt starter cultures require a symbiotic blend of *Lactobacillus delbrueckii* ssp. *bulgaricus* and *S. thermophilus* to achieve the desired organoleptic properties such as texture, acidity, and flavor (Oyeniran et al., 2020). *Streptococcus thermophilus* has urease genes and

Table 2. Abbreviations for dairy-related Lactobacilli

Genus	Abbreviation	Species; common source
<i>Lactobacillus</i> ¹	<i>Lb.</i>	<i>delbrueckii</i> ² <i>delbrueckii</i> ssp. <i>bulgaricus</i> ; yogurt, cheese <i>delbrueckii</i> ssp. <i>lactis</i> ; milk, cheese <i>delbrueckii</i> ssp. <i>indicus</i> ; fermented dairy product (dahi) <i>helveticus</i> ; sour milk, cheese, silage <i>acidophilus</i> ; no mention of isolation from dairy products other than use as starter. <i>kefiranofaciens</i> ssp. <i>kefirgranum</i> ; kefir grains, sour milk <i>kefiranofaciens</i> ssp. <i>kefiranofaciens</i> ; -kefir grains and other fermented dairy products <i>acetotolerans</i> ; silage <i>helsingborgensis</i> ; alfalfa silage <i>taiwanensis</i> ; silage <i>amylovorus</i> ; cattle waste-cord fermentation <i>casei</i> ² ; silage, most previous designations should be reclassified as <i>paracasei</i> <i>paracasei</i> <i>paracasei</i> ssp. <i>paracasei</i> ; dairy products and silage <i>paracasei</i> ssp. <i>tolerans</i> ; dairy products <i>rhamnosus</i> ; dairy products <i>nasuensis</i> ; grass silage <i>chiayiensis</i> ; cow manure
<i>Lacticaseibacillus</i> ¹	<i>Lcb.</i>	<i>plantarum</i> ; dairy fermentations <i>plantarum</i> ssp. <i>plantarum</i> ; dairy products and dairy environments, cow dung, silage <i>plantarum</i> ssp. <i>argenteratensis</i> ; elephant grass silage <i>paraplantarum</i> ; dairy products, sow milk, silage <i>pentosus</i> ; dairy products, corn silage
<i>Lactiplantibacillus</i> ¹	<i>Lpb.</i>	<i>sakei</i> ² <i>curvatus</i> ; dairy products such as milk and cheese, corn or grass silage, cow dung <i>graminis</i> ; grass silage <i>kefiri</i> ; kefir grains <i>parakefiri</i> ; kefir grains <i>buchneri</i> ² ; milk, cheese <i>parabuchneri</i> ; dairy products, silage <i>curiae</i> ; cheese curd powder <i>diolivorans</i> ; silage, fermented dairy products <i>hulgardii</i> ; silage <i>parafarraginis</i> ; silage, kefir grains <i>brevis</i> ² ; milk, cheese, silage, cow manure <i>parabrevis</i> ; cheese <i>angrenensis</i> ; fermented dairy beverage <i>hammesii</i> ; ryegrass silage <i>salivarius</i> ² ; dairy products <i>acidipiscis</i> ; dairy products <i>agilis</i> ; cheese <i>fermentum</i> ² ; dairy products, manure <i>pontis</i> ; dairy products, silage <i>gastricus</i> ; human milk <i>oris</i> ; human milk <i>reuteri</i> ; of intestinal origin, <i>bifermentans</i> ; cheese, fermented milk products <i>coryniformis</i> ² <i>coryniformis</i> ssp. <i>coryniformis</i> ; silage, dairy barn air and sewage. cow dung, cheese <i>coryniformis</i> ssp. <i>torquens</i> ; cheese, silage <i>renmini</i> ; rennet <i>iwatensis</i> ; orchard grass silage <i>hokkaidonensis</i> ; grass silage <i>vaccinostercus</i> ² ; cow dung <i>wasatchensis</i> ; cheese, silage <i>suebicus</i> ; silage <i>alimentarius</i> ² <i>crustorum</i> ; fermented dairy product <i>farciminis</i> ; dairy products, corn silage <i>zhongbaensis</i> ; fermented dairy product
<i>Latilactobacillus</i> ¹	<i>Lat.</i>	<i>amylophilus</i> ² <i>amylotrophicus</i> ; corn silage <i>concausus</i> ² <i>dextrinicus</i> ; silage
<i>Lentilactobacillus</i> ³	<i>Len.</i>	
<i>Levilactobacillus</i> ³	<i>Lev.</i>	
<i>Ligilactobacillus</i> ¹	<i>Lig.</i>	
<i>Limosilactobacillus</i> ³	<i>Lim.</i>	
<i>Loigolactobacillus</i> ¹	<i>Lo.</i>	
<i>Paucilactobacillus</i> ³	<i>Pa.</i>	
<i>Companilactobacillus</i> ³	<i>Co.</i>	
<i>Amylolactobacillus</i> ³	<i>Am.</i>	
<i>Lapidilactobacillus</i> ³	<i>Lap.</i>	

¹Homofermentative.²Species are the type species for this genus.³Heterofermentative.

its production of NH_3 has a stimulatory effect on *Lb. delbrueckii* ssp. *bulgaricus*, therefore, urease activity is an essential factor for effective yogurt acidification (Yamauchi et al., 2019). Many countries have legal requirements for the minimum number (such as $10^7/\text{g}$) of yogurt starter bacteria or viable lactobacilli, and for the ratio of *Lb. delbrueckii* ssp. *bulgaricus* to *S. thermophilus* (Oyeniran et al., 2020).

Fermented milks have a long history of production in many parts of the world and include kefir and koumiss, cultured buttermilk, mesophilic cultured milks such as ilmjolk, tatmjolk and langofil, thermophilic cultured milks such as Bulgarian buttermilk, zabadi, dahi, and biotherapeutic type products such as sweet acidophilus milk.

***Lactobacillus delbrueckii* ssp. *bulgaricus*.** *Lactobacillus delbrueckii* is the type species for the *Lactobacillus* genus. *Lactobacillus delbrueckii* ssp. *bulgaricus* ferments glucose to lactic acid and also metabolizes fructose, mannose, and lactose, but not galactose or sucrose. This subspecies was previously referred to as *Lactobacillus bulgaricus* and was originally isolated from yogurt (Zheng et al., 2020). *Lactobacillus delbrueckii* is the type species for the *Lactobacillus* genus. *Lactobacillus delbrueckii* ssp. *bulgaricus* ferments glucose to lactic acid and also metabolizes fructose, mannose and lactose, but not galactose or sucrose. This subspecies was previously referred to as *Lactobacillus bulgaricus* and was originally isolated from yogurt.

For use as a starter culture in yogurt, both the flavor production and acid-producing characteristics of *Lb. delbrueckii* ssp. *bulgaricus* are important. There are differences between strains of this species in terms of fermentation time, acidification rate, and acetaldehyde production. Natural selection pressure and the environmental stress conditions of yogurt can result in selection of strains yielding different acetaldehyde concentrations that can be an issue in yogurt manufacture (Liu et al., 2016). Some *Lb. delbrueckii* ssp. *bulgaricus* strains

produce extracellular polysaccharides, which act as food stabilizers to prevent syneresis and graininess, and provide the product with natural thickness (Cerning, 1990; Rizzello and De Angelis, 2011). *Lactobacillus delbrueckii* ssp. *bulgaricus* is also regarded as having probiotic properties (Oyeniran et al., 2020).

Strains of *Lb. delbrueckii* ssp. *bulgaricus* have also been a traditional starter culture for Swiss (Biede et al., 1977) and Italian cheeses although it is now often replaced by *Lactobacillus helveticus* (White et al., 2003), which has the ability to ferment galactose (Johnson and Olson, 1985). In the manufacture of Swiss cheese, the ratio of *Lb. delbrueckii* ssp. *bulgaricus* compared with *S. thermophilus* in the starter culture influences the chemistry and flavor of Swiss cheese through changes in its microbiota. Using *Lb. delbrueckii* ssp. *bulgaricus* increases flavor intensity, yet there is an optimum level above which numbers of propionibacteria decrease, which retards flavor development (Biede et al., 1977).

***Lactobacillus acidophilus*.** *Lactobacillus acidophilus* grows optimally at 35 to 40°C, but it is able to grow at temperatures as high as 45°C and is an homofermentative lactic acid bacterium producing lactic acid and carbon dioxide through the Embden-Meyerhof-Parnas pathway (Ozogul et al., 2022). The usual method for enumerating *Lb. acidophilus* in yogurt and other dairy products is with de Man, Rogosa, and Sharpe (MRS) agar (pH 5.4), incubated anaerobically at 45°C, which inhibits *S. thermophilus*; however, other lactobacilli that may be present in the product can grow in this medium (Ozogul et al., 2022).

In the United States, perhaps the first dairy food commercially manufactured and marketed for health promoting benefits was sweet acidophilus milk made using *Lb. acidophilus*. The higher pH of nonfermented products such as sweet acidophilus milk provides for longer survival. In mixed cultures, growth of *Lb. acidophilus* during fermentation is much slower than other

Table 3. Use of *Lactobacillus* as defined strain acid-producing starter cultures

Product	Organism	Usage	Reference
Yogurt	<i>Lb. delbrueckii</i> ssp. <i>bulgaricus</i> ¹	Often legally required in some countries	Aryana and Olson, 2017
Swiss and Dutch Cheeses	<i>Lb. delbrueckii</i> ssp. <i>bulgaricus</i> ¹ <i>Lb. delbrueckii</i> ssp. <i>lactis</i> ^{1,2} <i>Lb. helveticus</i> ¹	Traditional usage was <i>Lb. delbrueckii</i> ssp. <i>bulgaricus</i> but is now more frequently <i>Lb. helveticus</i>	Hunter and Frazier, 1961 Biede et al., 1977 Reddy and Richardson, 1977 White et al., 2003 Ji et al., 2004
Mozzarella Cheese	<i>Lb. delbrueckii</i> ssp. <i>bulgaricus</i> ³ <i>Lb. helveticus</i> ³	<i>Lb. helveticus</i> is often used as it has it is able to better ferment galactose	Biede et al., 1977 Johnson and Olson, 1985

¹Used in conjunction with *Streptococcus thermophilus*.

²Allows measurement of D- and L-lactate levels to monitor relative bacterial numbers.

³Either used with *S. thermophilus* or not used and cheese made using *S. thermophilus* only.

Table 4. Lactobacilli¹ that have been shown to be present in kefir grains

Predominant lactobacilli	Other lactobacilli	References
<i>Lb. kefiranofaciens</i> ssp. <i>kefiranofaciens</i>	<i>Lb. delbrueckii</i>	Wang et al., 2018
<i>Lb. kefiranofaciens</i> ssp. <i>kefirgranum</i>	<i>Lb. acidophilus</i>	Magalhães et al., 2010
	<i>Lev. brevis</i>	Vardjan et al., 2013
	<i>Lb. helveticus</i>	Huang et al., 2013
	<i>Lcb. casei</i>	Kandler et al., 1983
	<i>Lcb. paracasei</i>	
	<i>Lim. fermentum</i>	
	<i>Lpb. plantarum</i>	
	<i>Lb. gasseri</i>	
	<i>Len. sunkii</i>	
	<i>Len. kefiri</i>	
	<i>Len. parakefiri</i>	

¹Genus abbreviations as described in Table 2.

lactobacilli and *S. thermophilus*. Instability of *Lb. acidophilus* in yogurt can be caused by hydrogen peroxide production by other lactobacilli (Ozogul et al., 2022). When *Lb. acidophilus* is added in cheesemaking as an adjunct culture for its probiotic potential, its persistence during cheese aging can change the flavor profile of the cheese and, hence, its consumer acceptability (Gomes et al., 2011). Measurement of *Lb. acidophilus* persistence in cheese during its shelf life is difficult as many NSLAB can grow under the same conditions used to enumerate *Lb. acidophilus* (Oberge et al., 2011).

Lactobacillus acidophilus is also used in the manufacture of yogurt, yogurt drinks, iru-miru, kefir, fermented desserts, and koumiss (Ozogul et al., 2022). The organism is considered a probiotic bacterium for which a minimal level of viability for a specified strain in the product needs to be maintained if the product carries any type of health claim. Many *Lb. acidophilus* strains inhibit gram-positive and gram-negative bacteria, a result of production of a combination of hydrogen peroxide, organic acid, and bacteriocins such as lactocin B, lactacin F, acidocin A, and acidocin B (Ozogul et al., 2022).

***Lactobacillus kefiranofaciens*.** This homofermentative species produces lactic acid from a variety of sugars including glucose, fructose, galactose, sucrose, maltose, lactose and raffinose, but not from arabinose, ribose, cellobiose, or trehalose (Vancanneyt et al., 2004). Two subspecies are recognized: *Lactobacillus kefiranofaciens* ssp. *kefiranofaciens* and *Lactobacillus kefiranofaciens* ssp. *kefirgranum*.

Fermentation of milk using a combination of bacteria and yeasts (such as *Kluyveromyces marxianus*, *Saccharomyces cerevisiae*, and *Kazachantania unispora*) developed in central Asia (north of the Caucasus mountains) at least 2,000 years ago. Kefir and similar fermented milks have undergone continuous harvesting of the starter culture (Table 4) and propagation in homes since that time. Kefir grains resemble miniature cau-

liflower florets and consist of a symbiotic mixture of yeasts, lactobacilli, lactococci, and *Leuconostoc* species (Aryana and Olsen, 2017). The dominant and most consistent lactobacilli in kefir grains is *Lactobacillus kefiranofaciens* (Wang et al., 2018).

Kefir grains are held together by a complex mixture of protein and a polysaccharide (kefirin) that is a component of the capsular material of *Lentilactobacillus parakefiri* and *Lb. kefiranofaciens*, which are the major exopolysaccharide (EPS)-producing bacteria present in kefir grains (Kök-Tas et al., 2012). Certain strains of *Lb. kefiranofaciens* have demonstrated probiotic properties (Vinderola et al., 2006; Furuno and Nakanishi, 2012). Propagating the kefir grains in milk is important for maintaining the dominant lactobacilli otherwise other species begin to dominate (Zanirati et al., 2015). In traditional kefir, although lactic acid is the main fermentative metabolite, small amounts of alcohol and carbon dioxide are also produced by the yeast present in the kefir grain giving a pronounced effervescence typical of kefir.

***Lentilactobacillus kefiri*.** The genus *Lentilactobacillus* was so called because of the slow growth of species in the genus with lactate or propanediol as carbon source (Zheng et al., 2020). Formerly known as *Lactobacillus kefir* or *Lactobacillus kefiri*, this organism is mainly found as part of the microbiota of kefir grains and kefir drinks (Kandler et al., 1983) but has also been isolated from Camembert cheese, in ricotta forte (Baruzzi et al., 2000) and in raw camel milk (Akhmet-sadykova et al., 2015).

***Lentilactobacillus parakefiri*.** *Lentilactobacillus parakefiri* is very closely related to, but distinct from, *Len. kefiri*. A heterofermentative organism, it produces L-lactic acid, and CO₂ from glucose, but not from gluconate (Takizawa et al., 1994). It was originally isolated from kefir grains but has been recently identified as a predominant LAB in butter (Syromyatnikov et al., 2020).

***Lentilactobacillus sunkii*.** *Lentilactobacillus sunkii* has been isolated from kefir (Han et al., 2018), but was originally isolated from sunki, a type of Japanese pickle (Watanabe et al., 2009). It is a heterofermentative organism producing lactic acid and gas from glucose metabolism.

Species Associated with Cheese

***Lactobacillus helveticus*.** *Lactobacillus helveticus* is homofermentative. All strains of *Lb. helveticus* ferment glucose, galactose, and lactose, whereas some strains also ferment fructose, maltose, mannose and trehalose. *Lactobacillus helveticus* does not use pentoses, cellobiose, mannitol, raffinose, sucrose, or gluconate (Nikoloudaki et al., 2022).

Lactobacillus helveticus can be used in the manufacture of Swiss and Dutch style cheeses instead of *Lb. delbrueckii* ssp. *bulgaricus* because of its ability to ferment galactose. Another distinction is that *Lb. helveticus* produces both D- and L-lactate, whereas *Lb. delbrueckii* ssp. *bulgaricus* only produces the D-lactate isomer, which may be of advantage in Swiss cheese manufacture as the L-lactate isomer is preferred by propionibacteria (Nikoloudaki et al., 2022). Later, when placed in a warm room (~20 to 22°C) it is primarily L-lactate that is used by *Propionibacterium freudenreichii*, as this results in a high intracellular pyruvate concentration that inhibits D-lactate dehydrogenase activity (White et al., 2003).

The most commonly used lactobacilli now in the starter culture for Swiss cheese is *Lb. helveticus* (White et al., 2003; Ji et al., 2004), replacing *Lb. delbrueckii* ssp. *bulgaricus* (Reddy and Richardson, 1977). In Swiss cheese, *Lb. helveticus* is the secondary acid producer to *S. thermophilus*, provides proteolysis in the later stages of ripening, and contributes to flavor development.

During manufacture up until brining D- or L-lactic acid are essentially the only end products of lactose fermentation. After brining is when the selection of *Lb. helveticus* or *Lb. delbrueckii* ssp. *bulgaricus* has greater effect. For example, differences in their cell wall proteases result in Swiss cheese made using *Lb. helveticus* having greater stretchability than when made using *Lb. delbrueckii* ssp. *lactis* (Richoux et al., 2009; Sadat-Mekmene et al., 2013).

In the whey culture (Table 5) used for manufacture of Italian cultures hard cheeses such as Parmigiano Reggiano, the dominant species is *Lb. helveticus* along with *Lb. delbrueckii* ssp. *bulgaricus*, *Lb. delbrueckii* ssp. *lactis*, *Lacticaseibacillus casei*, *Limosilactobacillus fermentum*, and *S. thermophilus* (Reinheimer et al., 1995; Gatti et al., 2003; Bottari et al., 2010). In Argentina, the whey starter used for Reggianito Argentino cheese consisted of ~66% *Lb. helveticus* strains and ~33% of *Lb. delbrueckii* ssp. *lactis* (Reinheimer et al., 1996). Various biotypes occur in *Lb. helveticus* strains in whey starters with differences in fructose, maltose, and trehalose fermentation, acidifying activity, proteolytic and peptidase activity, and antibiotic and lysozyme resistance (Fortina et al., 1998). Often a characteristic of such whey starters is a low salt tolerance of the strains (Reinheimer et al., 1996). Replacement of the whey starter with defined strains of *Lb. helveticus* can produce cheese with comparable flavor, and Hynes et al. (2003) found that such cheeses did not group by *Lb. helveticus* strain or type of starter when analyzed for flavor. *Lactobacillus helveticus* is used as a flavor adjunct (Table 6) in Cheddar manufacture adds sweet-nutty aspects to the flavor profile and prevents bitterness (Madkor et al., 2000).

***Lactobacillus delbrueckii* ssp. *lactis*.** This subspecies of *Lb. delbrueckii* has traditionally been one of the lactobacilli used as a starter culture in Swiss-type

Table 5. Lactobacilli¹ identified as part of in-factory propagated whey starter cultures

Cheese type (location)	Predominant bacteria	Other bacteria	Reference
Gruyère Emmental Grana (France, Switzerland, Italy)	<i>Streptococcus thermophilus</i>	<i>Lactococcus</i> sp. <i>Leuconostoc</i> sp. <i>Lb. helveticus</i> <i>Lb. delbrueckii</i> <i>Lb. acidophilus</i> <i>Lim. fermentum</i>	Beresford et al., 2001
Parmigiano Reggiano (Italy)	<i>Lb. helveticus</i>	<i>Lb. delbrueckii</i> ssp. <i>bulgaricus</i> <i>Lb. delbrueckii</i> ssp. <i>lactis</i> <i>Lcb. casei</i> <i>Lim. fermentum</i> <i>S. thermophilus</i>	Beresford et al., 2001 Nikoloudaki et al., 2022 Reinheimer et al., 1995 Gatti et al., 2003 Bottari et al., 2010 Reinheimer et al., 1996
Reggianito Argentino (Argentina)	<i>Lb. helveticus</i> <i>Lb. delbrueckii</i> ssp. <i>lactis</i>		Bottari et al., 2010 Reinheimer et al., 1996
Caciocavallo Silano and Grana Padano cheeses (Italy)	<i>Lim. fermentum</i>		Rossetti et al., 2008

¹Genus abbreviations as described in Table 2.

Table 6. Historical view of nonstarter lactobacilli¹ in Cheddar cheese

Time period	Country	Dominant Lactobacilli	Other Lactobacilli present	Reference
1930s 1960s 1990s	New Zealand United Kingdom	<i>Lpb. plantarum</i> <i>Lcb. casei/paracasei</i> <i>Lcb. casei/paracasei</i> <i>Lpb. plantarum</i>	<i>Lcb. paracasei/casei</i> ² <i>Lpb. plantarum</i> , <i>Lev. brevis</i> <i>Lat. curvatus</i> , <i>Lev. brevis</i> <i>Lb. helveticus</i> , <i>Lim. fermentum</i> , <i>Lo. bifementans</i> , <i>Len. buchneri</i> , <i>Len. parabuchneri</i> , <i>Len. kefir</i> <i>Co. farciminis</i>	Peterson and Marshall, 1990 Peterson and Marshall, 1990 Williams and Banks, 1997
2020	USA and Ireland	<i>Lcb. paracasei</i> <i>Lcb. rhamnosus</i> <i>Lcb. delbrueckii</i> ³ <i>Lb. helveticus</i> ³ <i>Lat. curvatus</i> <i>Pa. wasatchensis</i> <i>Se. malefermentans</i>	<i>Lcb. casei</i> , <i>Lcb. paracasei</i> <i>Lcb. rhamnosus</i> <i>Lpb. plantarum</i> <i>Lb. delbrueckii</i> , <i>Lb. helveticus</i> <i>Lb. hokkaidonensis</i> , <i>Lb. crispatus</i> <i>Lat. curvatus</i> <i>Len. buchneri</i> , <i>Len. farraginis</i> <i>Len. kefir</i> , <i>Len. kisonensis</i> <i>Pa. wasatchensis</i> , <i>Lo. coryniformis</i> , <i>Lo. coryniformis ssp. torquens</i>	Overbeck, 2021

¹Genus abbreviations as described in Table 2.

²Many species classified previously (before ~1990) as *Lactobacillus casei* were most likely *Lactobacillus paracasei* (Minervini and Calasso, 2020), and most genomes designated as *Lb. casei* in the National Center for Biotechnology Information database (<https://ncbi.nlm.nih.gov>) database should be classified as *Lb. paracasei* as well (Zheng et al., 2020).

³Possibly added as an adjunct starter culture.

cheeses along with *Lb. delbrueckii* ssp. *bulgaricus* and *Lb. helveticus* (Hunter and Frazier, 1961). *Lactobacillus delbrueckii* ssp. *lactis* is also used as a starter culture in Emmental and Gruyère-type cheeses (Weinrichter et al., 2004). Traditional production Ragusano cheese in Italy use wooden vessels that carry a biofilm on their surface that inoculates and acidifies the milk. The dominant species in these biofilms are *S. thermophilus* and *Lb. delbrueckii* ssp. *lactis* (Licitra et al., 2007).

LACTOBACILLI ISOLATED FROM MILK AND DAIRY PRODUCTS

In products such as cheese, there is a secondary microbiota that develops during product ripening and storage, which can consist of complex mixtures of bacteria, yeasts, and molds, depending on the particular cheese variety (Beresford et al., 2001). Before the onset of DNA sequencing technologies to identify NSLAB in cheese, only those bacteria that could be cultured from the cheese were identified (Table 6). Some traditional cheeses made without addition of any starter culture rely upon endogenous lactic acid bacteria in the raw milk to bring about fermentation (Efthymiou and Mattick, 1964; Di Cagno et al., 2007). Such cheeses typically contain both homofermentative and heterofermentative lactic acid bacteria including *Lacticaseibacillus paracasei*, *Lactiplantibacillus plantarum*, and *Levilactobacillus brevis*, generally considered NSLAB (Di Cagno et al.,

2007). These NSLAB lactobacilli can be isolated, characterized, then used as adjunct cultures (Table 7) to the starter cultures to provide added benefits to the final product such as enhanced flavor, more rapid flavor development, and even inhibition of undesirable bacteria during storage.

Adjunct cultures can also be attenuated (such as by freezing, drying, or heat shocking) to provide a mixture of viable and nonviable bacterial cells. Use of adjunct cultures (Table 7) must be considered on an individual basis because of wide strain diversity, such as the ability of strains of *Lacticaseibacillus casei* and *Lacticaseibacillus paracasei* to metabolize amino acids in cheese into flavor compounds (Stefanovic et al., 2017a). Among lactobacilli isolated from cheese, some can grow and ferment milk relatively quickly (reaching pH 4.5 within 8 h at 34°C), whereas others are slow strains that required supplementation with glucose or casein hydrolysate, and even with supplementation, some strains still do not grow in milk (Briggiler-Marcó et al., 2007). Selecting strains that have little effect on acidification would be preferred for use as a flavor adjunct culture so as to not interfere with the time schedule during cheese manufacture.

The genus *Lacticaseibacillus* is homofermentative; some but not all species metabolize pentoses via the phosphoketolase pathway (Zheng et al., 2020). In addition to their use as adjuncts, several *Lacticaseibacillus* species are used as starter cultures in dairy fermentations and as probiotics.

Table 7. Lactobacilli^{1,2} used as adjunct cultures in cheese

Bacteria	Purpose	References
<i>Lcb. casei</i> <i>Lcb. paracasei</i>	Flavor, probiotic, control of other bacteria	Minervini and Calasso, 2020 Lynch et al., 1996 Kocaoglu-Vurma et al., 2008
<i>Lcb. rhamnosus</i>	Preventing bitterness, control of other heterofermentative lactobacilli that can cause late blowing, biopreservative	Kocaoglu-Vurma et al., 2008 Laleye et al., 1989
<i>Lpb. plantarum</i>	Flavor	Lynch et al., 1996
<i>Lb. helveticus</i>	Add sweet nutty flavor to Cheddar cheese	Madkor et al., 2000
<i>Co. nodensis</i>	Increase sulfur flavor notes	O'Brien et al., 2017

¹Genus abbreviations as described in Table 2.

²Beneficial and detrimental effects of adjunct cultures are strain dependent (Stefanovic et al., 2017a).

Adjunct Species Associated with Cheese

***Lacticaseibacillus casei*.** The genus name of *Lacticaseibacillus* refers to the casei-group lactobacilli with *Lcb. casei* being differentiated from most lactobacilli by many strains exhibiting catalase activity (Wuyts et al., 2017). Information on the lifestyle of *Lcb. casei* is confounded by the unclear taxonomy during the past decades. In dairy literature before 1989, many strains then classified as *Lactobacillus casei* were probably *Lcb. paracasei* (Minervini and Calasso, 2020) and most genomes designated as *Lcb. casei* in the National Center for Biotechnology Information database (<https://ncbi.nlm.nih.gov>) should instead be classified as *Lcb. paracasei* (Zheng et al., 2020).

Although first isolated from cheese, *Lcb. casei* is widely distributed in diverse habitats including decaying plant material, silage, and the human reproductive and gastrointestinal tracts. Because of its aciduric nature, it is also found in many fermented foods of both plant (e.g., fermented vegetables, sourdough, wine) and animal (e.g., dairy products, cured meat, fermented sausages) origin (Minervini and Calasso, 2020). *Lacticaseibacillus casei* has been most often identified as the main adventitious bacteria (NSLAB) present and growing in ripening cheese, although this is a distinction it now shares with *Latilactobacillus curvatus* (Broadbent et al., 2003).

The use of selected strains of *Lcb. casei* as adjuncts for cheese ripening or as probiotic cultures in various foods has been continually increasing. Depending on the strain, *Lcb. casei* can contribute to positive flavor attributes of cheese, to defects, or have no effect on cheese ripening, which is also influenced by cell density and the cheesemaking technology (Minervini and Calasso, 2020).

Using a homofermentative lactobacilli as an adjunct culture (such as *Lcb. casei*, *Lcb. paracasei*, and *Lactiplantibacillus plantarum*) can inhibit growth of heterofermentative lactobacilli such as *Levilactobacillus*

brevis and *Limosilactobacillus fermentum* (Laleye et al., 1989). Adding the adjunct culture, *Lcb. casei*, when making cheese can also change the initial NSLAB biota resulting in a reduction in nonstarter species and strain diversity (Broadbent et al., 2003).

***Lacticaseibacillus paracasei*.** *Lacticaseibacillus paracasei* includes strains previously referred to as *Lactobacillus casei* ssp. *alactosus*, *Lactobacillus casei* ssp. *pseudopantarum*, and *Lactobacillus casei* ssp. *tolerans* (Zheng et al., 2020). Growth of *Lcb. paracasei* generally occurs over the range of 10 to 40°C, but some strains can grow at 5°C and some up to 45°C. *Lacticaseibacillus paracasei* cannot ferment rhamnose which distinguishes it from *Lacticaseibacillus rhamnosus* (Minervini and Calasso, 2020).

Although not as proteolytic as *Lb. helveticus*, most strains of *Lcb. paracasei* have at least one cell envelope-associated serine-type proteinase involved in the breakdown of casein. Enzyme specificity and profile of oligopeptide products produced is strain dependent. Proteinases from *Lcb. paracasei* (and *Lcb. rhamnosus*) are more suited for the salt and pH conditions in cheese, so they are less inhibited than lactococcal proteinases. When some strains are used as adjunct cultures, improved cheese flavor is usually accompanied by altered proteolysis leading to higher concentrations of amino acids and small peptides, and changes in the cheese peptide profile. Other strains can produce a bitter defect in cheese (Minervini and Calasso, 2020).

In raw milk cheeses, NSLAB, especially heterofermentative lactobacilli such as the *Lacticaseibacillus* and *Lactiplantibacillus*, can grow from initial levels of 10² cfu/g during storage to levels 10⁶ to 10⁸ cfu/g in cheeses that have a warm ripening stage to promote growth and activity of propionibacteria (Weinrichter et al., 2004). Often raw milk cheeses will vary in quality throughout the year as changes occur in the NSLAB population in the milk. To ensure the preferred NSLAB microbiota is present in the cheese, NSLAB can be isolated from good quality cheese and those strains used as an

adjunct culture in future cheese production. Adding adjunct lactobacilli, even those derived from the NSLAB microbiota, above levels of 10^4 cfu/mL tends to produce atypical flavors during cheese ripening (Peterson and Marshall, 1990).

Lacticaseibacillus rhamnosus. *Lacticaseibacillus rhamnosus* has a nomadic lifestyle being found in a broad range of habitats including dairy products, fermented meat, fish, vegetables and cereals, sewage, humans (oral, vaginal, and intestinal), invertebrate hosts and clinical sources (Zheng et al., 2020). *Lacticaseibacillus rhamnosus* is also used as an adjunct culture to prevent spoilage in dairy products (Makki et al., 2020).

Companilactobacillus nodensis. The genus *Companilactobacillus* refers to the association of *Companilactobacillus* species with other lactobacilli, particularly heterofermentative organisms, in cereal and vegetable fermentations (Zheng et al., 2020). *Companilactobacillus nodensis* was originally isolated from Japanese pickles (Kashiwagi et al., 2009) and has been detected in a Danish raw milk cheese where metabolically active bacteria during the ripening process were identified (Masoud et al., 2012). The species uses pentoses and hexoses, but not disaccharides, as carbon sources. The strain CSK964 was shown to produce volatile sulfur compounds including hydrogen sulfide. The strain was subsequently tested as a flavor adjunct in Gouda cheese, where hydrogen sulfide and methanethiol were present in higher abundances in cheeses containing the strain CSK964 of this species (O'Brien et al., 2017).

Other Lactobacilli Isolated from Milk and Dairy Products

Apart from the starter culture bacteria (*L. lactis* and *S. thermophilus*) lactobacilli comprise the majority of NSLAB present in cheese (Overbeck, 2021). Depending on the species and strain, their metabolic activity may contribute to defects or inconsistency in cheese quality and development of typical cheese flavor (Blaya et al., 2018). In Cheddar cheese, they are present initially at only 10^4 cfu/g or less but increase to 10^6 to 10^8 cfu/g within a few months (Peterson and Marshall, 1990; Blaya et al., 2018). However, although the adjunct culture may initially dominate (e.g., 10^5 cfu/g compared with NSLAB numbers of typically $\leq 10^2$ cfu/g in high quality cheese) with longer aging periods it is the wild type lactobacilli (lactobacilli not intentionally added to the milk) that dominate. In higher moisture cheese such as part skim Mozzarella or Scamorza cheese, this increase may occur within 1 mo (Guidone et al., 2015). Lactobacilli are common contaminants of raw milk but

generally make up only a small proportion of the raw milk microbiota ((Minervini and Calasso, 2020). Most do not survive pasteurization but some species such as *Lacticaseibacillus paracasei* ssp. *tolerans* can survive as well as some other strains of *Lcb. paracasei* which would be present in cheese milk at low levels.

Initial numbers of NSLAB in cheese are influenced by their numbers in raw milk (especially if pasteurization is not used) and the extent of postpasteurization contamination from biofilm buildup in processing equipment and pipelines. The environment inside individual dairy factories becomes the permanent habitat for strains of lactobacilli that can differ from facility to facility. Such lactobacilli thus replace the heat-sensitive lactobacilli present in raw milk, and may impart individual flavor characteristics to cheese made in a particular factory (Peterson and Marshall, 1990). The presence of such NSLAB in factories that produce high quality cheese appear to have a beneficial effect on generating good Cheddar cheese flavor during the aging process and these NSLAB isolates have been used as adjunct cultures to improve flavor development during ripening (Reiter et al., 1965; Law et al., 1976; Peterson and Marshall, 1990; Lynch et al., 1996).

Numerous lactobacilli are also part of plant fermentations and have been isolated from silage use as feed (Zheng et al., 2020). These organisms, although not used in dairy fermentations, are an important source of spoilage in dairy products. A list of some of these are given in Table 8. Many lactobacilli are also used as starter cultures for silage such as *Lentilactobacillus* species (e.g., *Lentilactobacillus buchneri*), which are then isolated from dairy products. Many other lactobacilli have been isolated from dairy products, but are not used as starters, adjuncts, or associated with dairy silage. These organisms originate from environmental sources and are listed in Table 9.

Lactiplantibacillus plantarum. The genus *Lactiplantibacillus* is the previous plantarum-group lactobacilli with the name referring to their association with both milk and plants (Zheng et al., 2020). *Lactiplantibacillus plantarum* is a dominant member of the microbiota in spontaneous vegetable and olive fermentations, and also occurs in sourdough, dairy fermentations, and fermented meats. It can also be isolated from the human intestinal tract, including the oral cavity (Zheng et al., 2020).

From the 1930s until recently (Table 6) a dominant NSLAB isolated from cheese in New Zealand, the United Kingdom and the United States was *Lpb. plantarum* (Peterson and Marshall, 1990; Williams and Banks, 1997). In the traditional manufacture of Oaxaca cheese in Mexico, raw milk is used without any starter

Table 8. Lactobacilli species isolated from silage (Zheng et al., 2020)

Genus	Species
<i>Lactobacillus</i>	<i>acetotolerans</i> , <i>helsingborgensis</i> , <i>helveticus</i> , <i>taiwanensis</i>
<i>Lactocaseibacillus</i>	<i>casei</i> , <i>paracasei</i> ssp. <i>paracasei</i> , <i>paracasei</i> ssp. <i>tolerans</i> , <i>manihotivorans</i> , <i>nasuensis</i>
<i>Lactiplantibacillus</i>	<i>plantarum</i> ssp. <i>plantarum</i> , <i>plantarum</i> ssp. <i>argentoratensis</i> , <i>pentosus</i>
<i>Lapidilactobacillus</i>	<i>dextrinicus</i>
<i>Latilactobacillus</i>	<i>curvatus</i> , <i>graminis</i>
<i>Lentilactobacillus</i>	<i>buchneri</i> , <i>diolivorans</i> , <i>hilgardii</i> , <i>parabuchneri</i> , <i>parafarraginis</i>
<i>Levilactobacillus</i>	<i>brevis</i> , <i>hammesii</i>
<i>Limosilactobacillus</i>	<i>pontis</i>
<i>Loigolactobacillus</i>	<i>coryniformis</i> ssp. <i>coryniformis</i> , <i>coryniformis</i> ssp. <i>torquens</i> , <i>iwatensis</i> , <i>paraplantarum</i>
<i>Amylolactobacillus</i>	<i>amylotrophicus</i>
<i>Paucilactobacillus</i>	<i>hokkaidonensis</i> , <i>suebicus</i> , <i>vaccinostercus</i> , <i>wasatchensis</i>
<i>Companilactobacillus</i>	<i>formosensis</i>
<i>Secundilactobacillus</i>	<i>mixtipabuli</i> , <i>pentosiphilus</i> , <i>silage</i> , <i>silagincola</i>

culture addition (De Oca-Flores et al., 2009) and the predominant lactobacilli isolated from such cheeses are various strains of *Lpb. plantarum* (Caro et al., 2013).

Likewise, when strains of *Lpb. plantarum* (with broad-spectrum antibacterial activity in fermented milk) were added to yogurt, differences in volatile flavor compounds (such as 2,3-pentanedione, acetaldehyde and acetate) and texture were noted (Li et al., 2017). Several *Lpb. plantarum* EPS-producing strains have been isolated from various fermented foods as well as from kefir (Wang et al., 2018).

Lactiplantibacillus paraplantarum. *Lactiplantibacillus paraplantarum* is mostly associated with beer spoilage and vegetable fermentations, but can be found as part of the starter culture used for Beyaz cheese production (Karahana et al., 2010), and as part of the microbiota in ricotta forte cheese (Baruzzi et al., 2000), in Feta cheese (Manolopoulou et al., 2003), and in Tahana, a traditional fermented Turkish product composed of spontaneously fermented yogurt and wheat flour (Sengun et al., 2009) and in silage (Pang et al., 2011). A homofermentative species, they produce lactic acid from glucose. Researchers have experimented with purposely adding these bacteria isolated from nondairy sources into cheese with the aim of modifying flavor (Cioca et al., 2013). All strains ferment lactose and galactose (Curk et al., 1996).

Latilactobacillus curvatus. The name of the genus *Latilactobacillus* refers to the bacteria having a wide-spread range of habitats, which is the case for *Lat. curvatus*, which has been isolated from a wide variety of environments including milk, cheese, fermented meat, fish and vegetable products, honey, corn and grass silage, and cow dung among others (Torriani et al., 1996; Terán et al., 2018). Lactic acid is produced from the fermentation of most hexoses and some pentoses, but it cannot ferment xylose. It is a member of the NSLAB population of many cheese varieties and can grow to high numbers in hard and semi-hard cheeses,

especially in Cheddar, Emmental, and Gruyère. Indeed, the organism is now the most common NSLAB found in cheese in North America (Broadbent et al., 2003). The species has been shown to be associated with gas-related defects (Porcellato et al., 2015) and an increase in calcium lactate crystal formation (Chou et al., 2003) in Cheddar cheese and with the production of biogenic amines (Barbieri et al., 2019). Other strains have shown probiotic potential as feed additives (Hong et al., 2018).

In a study using strains of *Lcb. casei*, *Lcb. paracasei*, *Lpb. plantarum*, and *Lat. curvatus* isolated from a good quality raw milk Cheddar cheese, the cheese made with *Lcb. paracasei* or *Lpb. plantarum* produced cheeses with the best flavor (Lynch et al., 1996). Interestingly, strains of both of these species of lactobacilli died off during storage whereas the *Lcb. casei* and *Lat. curvatus* persisted at high numbers during storage.

Lentilactobacillus buchneri. This species has been isolated from milk, some cheese varieties including Swiss-type cheese (Sumner et al., 1985), Canestrato Pugliese and ricotta forte, kefir, and traditional fermented dairy products such as qula (Zhang et al., 2016) and kurut (Sun et al., 2010), and is used as a silage inoculant (Muck et al., 2018). The species is associated with biogenic amine formation (Diaz et al., 2016). End products of fermentation of this heterofermentative species include lactic acid, acetic acid, ethanol, and carbon dioxide. They are also capable of producing 1,2-propanediol from lactic acid, and variously ferment esculin, galactose, lactose, raffinose, sucrose, xylose, and melezitiose (Pot et al., 2014).

Both *Lentilactobacillus buchneri* and *Lentilactobacillus parabuchneri* are common parts of the microbiome of cheeses, especially farmhouse cheeses (Fröhlich-Wyder et al., 2013). Although *Len. buchneri* was considered as a spoilage organism, its ability to anaerobically convert lactic acid into acetic acid and 1,2-propanediol led to its use as a silage inoculant (Holzer et al., 2003). The presence of *Len. buchneri* in cheese has been as-

Table 9. Other lactobacilli¹ that have been associated with dairy foods

Isolated species	Dairy product	Attribute	Reference
<i>Lb. delbrueckii</i> ssp. <i>indicus</i>	Isolated from Dahi, a fermented dairy product from India	Metabolizes sucrose, fructose, lactose and mannose, but is unable to ferment maltose and trehalose	Dellaglio et al., 2005
<i>Lb. sakei</i>	Isolated from raw milk Oaxaca cheese in Mexico		Caro et al., 2013
<i>Lb. diolivorans</i>	Isolated from raw milk and cheese, kefir and maize silage	Has high tolerance for solvents, and can produce 1,3 propanediol and 3-hydroxypropionate from glycerol, propanol and propionate from propanediol, and 2-butanol from meso-2,3-butanediol	Agostini et al., 2018 Abatemarco et al., 2018 Russmayer et al., 2019
<i>Lpb.</i> <i>paraplantarum</i>	Part of the starter culture used for Beyaz cheese production; isolated from ricotta forte cheese, Feta cheese and in Tahana, a traditional fermented Turkish product composed of spontaneously fermented yogurt and wheat flour product and in silage	Homofermentative; produces lactic acid from glucose and also ferment lactose and galactose	Karahan et al., 2010 Baruzzi et al., 2000 Manolopoulou et al., 2003 Sengun et al., 2009 Pang et al., 2011
<i>Lpb. pentosus</i>	Isolated raw bovine milk, fermented goat's milk and Brazilian artisanal cheese	Homofermentative; produces lactic acid from glucose and also ferment lactose and galactose	Agostini et al., 2018 Cho et al., 2018
<i>Lat. curvatus</i>	Part of the nonstarter lactic acid bacteria microbiota of many cheeses and often the dominant lactobacilli	Lactic acid is produced from most hexoses and some pentoses and disaccharides; does not ferment xylose Can promote calcium lactate crystal formation	Broadbent et al., 2003 Chou et al., 2003
<i>Len. sunkii</i>	Isolated from kefir	Heterofermentative; produces gas from glucose; produces, both lactic acid	Han et al., 2018
<i>Len. hilgardii</i>	Primarily associated with silage inoculation; found as part of the NSLAB population of white-brined cheeses made from goat's or sheep's milk		Ávila et al., 2014.
<i>Len. kefiri</i>	Isolated from Camembert and ricotta forte cheeses and in raw camel milk		Baruzzi et al., 2000 Akhmetsadykova et al., 2015 Syromyatnikov et al., 2020
<i>Len. parakefiri</i>	A predominant lactic acid bacteria in butter purchased in Russia		
<i>Len. buchneri</i>	Isolated from milk, Swiss, Canestrato Pugliese and ricotta forte, kefir, and traditional fermented dairy products such qula and kurut	Associated with biogenic amine formation. Used as silage inoculant; can produce 1,2-propanediol from lactic acid	Sumner et al., 1985 Zhang et al., 2016 Sun et al., 2015 Muck et al., 2018 Diaz et al., 2016
<i>Len.</i> <i>parabuchneri</i>	Isolated from raw milk and artisanal cheeses, Camembert and Parmigiano Reggiano cheeses	Responsible for accumulation of histamine in many cheeses; heterofermentative and forms CO ₂ from, hexoses.	Agostini et al., 2018 Guarcello et al., 2016 Henri-Dubernet et al., 2008 Gala et al., 2008 Wüthrich et al., 2017 Vancanneyt et al., 2006 Agostini et al., 2018
<i>Len. otakiensis</i>	isolated from bovine raw milk and artisanal cheese from southern Brazil	Heterofermentative; both lactic acid are produced, and gas is produced from glucose	
<i>Lev. brevis</i>	Isolated from Cheddar cheese, many artisanal dairy products and in raw camel's milk	Some strains produce high levels of γ -aminobutyric acid; heterofermentative	Fitzsimons et al., 1999 Gantzias et al., 2020 Sokovic Bajic et al., 2019 Carafa et al., 2019 Derriche et al., 2021 Vancanneyt et al., 2006
<i>Lev. parabrevis</i>	Originally isolated from a farmhouse red Cheshire cheese	Heterofermentative and produces CO ₂ from glucose and gluconate	
<i>Lev.</i> <i>angrenensis</i>	Isolated from traditional yogurt in Tibet	Heterofermentative; ferments and produces gas from glucose; ferments galactose but not from lactose	Long et al. 2020
<i>Lig. agilis</i>	Isolated from traditional Iranian cheeses	Acid is produced from glucose, galactose and lactose with weak reaction on pentoses	Ehsani et al., 2018 Baele et al., 2001

Continued

Table 9 (Continued). Other lactobacilli¹ that have been associated with dairy foods

Isolated species	Dairy product	Attribute	Reference
<i>Lig. acidipiscis</i>	Isolated from Mexican cheeses such as Cotija and double cream Chiapas cheese and traditional Greek Kopanisti cheese as well as silage	Homofermentative, and halotolerant, produces lactic acid from glucose; contributes to the volatile flavor compounds in cheese	Morales et al., 2011 Kazou et al., 2018
<i>Lim. pontis</i>	Isolated from a raw milk Piedmont cheese made from raw milk and corn silage		Bautista-Gallego et al., 2014 Han et al., 2014
<i>Lim. fermentum</i>	Ragusano and Manchego cheeses	Heterofermenter with sugar fermentation being strain dependent	Randazzo et al., 2002 Sánchez et al., 2006 Dellaglio et al., 2004
<i>Lo. rennini</i>	Isolated from calf rennet; associated with cheese spoilage and isolated from a traditional Greek overripened Kopanisti cheese called Mana	Homofermentative, no gas is produced from glucose or gluconate produces lactic acid	Chenoll et al., 2006 Kazou et al., 2018
<i>Lo. bifermentans</i>	Causes small cracks and gas formation in Edam and Gouda; isolated from Himalayan fermented milks	Heterofermentative with end lactic acid, acetic acid, ethanol, traces of propionic acid, carbon dioxide and free H ₂ as some of the end products of fermentation	Kandler et al., 1983 Dewan and Tamang, 2007
<i>Lo. coryniformis</i>	Isolated goat's milk cheese, Castelmagno cheese, Feta cheese, silage and cow dung	<i>Lo. coryniformis</i> ssp. <i>coryniformis</i> produces lactic acid from glucose	Martín et al., 2005 Dolci et al., 2008 Rantsiou et al., 2008 Wu et al., 2014
<i>Co. zhongbaensis</i>	Isolated from a Tibetan yogurt	Homofermentative; ferments glucose, lactose and galactose	Wei and Gu, 2019
<i>Sc. shenzhenensis</i>	Isolated from a fermented dairy beverage in China	Heterofermentative species; ferments lactose and galactose but not glucose	Zou et al. 2013
<i>Se. collinoides</i>	Isolated from traditional Iranian dairy products		Karami et al., 2017
<i>Co. crustorum</i>	First isolated from koumiss; also isolated from raw bovine milk and traditional Iranian dairy products	β -glucuronidase activity observed in some strains; cannot ferment pentoses; disaccharide fermentation is strain dependent	Danova et al., 2005 Yi et al., 2016 Qian et al., 2018 Sharafi et al., 2015
<i>Pa. wasatchensis</i>	Isolated from gassy Cheddar cheeses	Uses ribose to support growth and produces CO ₂	Oberg et al. 2016 Culumber et al., 2017 McMahon et al., 2020

¹Genus abbreviations as described in Table 2.

sociated with excessive histamine production, resulting in histamine poisoning upon consumption of an aged Swiss-type cheese (Sumner et al., 1985). Production of histamine by *Len. buchneri* and *Len. parabuchneri* is strain dependent, and some strains can also produce gamma-aminobutyric acid (Fröhlich-Wyder et al., 2013).

***Lentilactobacillus parabuchneri*.** This species is closely related to *Len. buchneri* and has been isolated from raw milk and artisanal cheeses (Agostini et al., 2018; Guarcello et al., 2016), Camembert cheese (Henri-Dubernet et al., 2008), Parmigiano Reggiano cheese (Gala et al., 2008) and silage, spoiled beer, and whiskey mashes. The organism is mainly responsible for the accumulation of histamine in many types of cheese (Wüthrich et al., 2017). A heterofermentative organism, hexoses are fermented to lactic acid, acetic acid, ethanol, and carbon dioxide (Vancanneyt et al., 2006).

***Limosilactobacillus fermentum*.** The genus *Limosilactobacillus* refers to the property of most strains in the genus to produce exopolysaccharides from su-

crose and hence being a slimy lactobacillus (Zheng et al., 2020). *Limosilactobacillus fermentum* includes strains previously classified as *Lactobacillus cellobiosus* (Dellaglio et al., 2004), and is one of the most abundant species in natural whey starters for Caciocavallo Silano, a hard 'pasta filata' cheese, and Grand Padano cheese (Rossetti et al., 2008). It is also often part of the nonstarter biota of certain cheeses including Ragusano (Randazzo et al., 2002), Manchego (Sánchez et al., 2006), and Swiss Comté (Cremonesi et al., 2011). Most often associated with cereal rather than dairy fermentations, the species has also been found in manure and in the rumen of young calves (Marounek et al., 1988). Some strains exhibit probiotic properties (Pastor-Villaescusa et al., 2020). A heterofermenter, sugar fermentation is strain dependent (Dellaglio et al., 2004).

Some *Lim. fermentum* are able to produce EPS which can be secreted into the medium (slime EPS) or remain attached to the cell wall (capsular polysaccharides). The EPS-producing bacteria have been used in the manufacture of fermented milk such as yogurt to

reduce syneresis and to modify the texture of cheeses (Ale et al., 2020). *Limosilactobacillus fermentum* has also been considered for probiotic use (de Souza et al., 2019). In the small-scale production of Gruyère, Emmental, and Grana cheeses of France, Switzerland, and Italy, whey starter culture incubated from the previous day is composed primarily of *S. thermophilus* but may also contain several species of lactobacilli such as *Lb. helveticus*, *Lb. delbrueckii*, *Lb. acidophilus*, and *Lim. fermentum* (Beresford et al., 2001; Nikoloudaki et al., 2022).

***Lactiplantibacillus pentosus*.** This organism has been isolated from varied sources including raw bovine milk (Agostini et al., 2018), fermented goats milk (Cho et al., 2018) and Brazilian artisanal cheese (Agostini et al., 2018). Some strains have exhibited probiotic properties (Ye et al., 2020). A heterofermentative species, it produces lactic acid from glucose. Acid is also produced from galactose and lactose (Zanoni et al., 1987).

***Levilactobacillus brevis*.** The genus *Levilactobacillus* refers to its leavening effect when used in sourdough bread (Zheng et al., 2020). *Levilactobacillus brevis* is primarily associated with spoiled beer and with sourdough and silage fermentations, but it has also been found among the NSLAB population of Cheddar cheese (Fitzsimons et al., 1999), many artisanal dairy products (Gantzias et al., 2020; Sokovic Bajic et al., 2019; Carafa et al., 2019), and in raw camel's milk (Derriche et al., 2021). High levels of γ -aminobutyric acid production are observed for some strains (Sokovic Bajic et al., 2019). In Greek Feta cheese, *Lev. brevis* is found along with *Lpb. plantarum*, *Lo. coryniformis* and *Lim. fermentum* (Rantsiou et al., 2008). A heterofermentative species, it utilizes hexoses by the 6-phosphogluconate pathway, producing lactic acid, CO₂ and ethanol or acetic acid in equimolar amounts (Orla-Jensen, 1919).

***Levilactobacillus parabrevis*.** *Levilactobacillus parabrevis* was originally isolated from a farmhouse red Cheshire cheese and was originally deposited in the NCFB culture collection as *Lactobacillus brevis* (Vancanneyt et al. 2006). The species produces lactic acid heterofermentatively with acetic acid and ethanol as other metabolites from glucose. Gas is produced from glucose and gluconate. Acid production from galactose and lactose is strain dependent.

***Lactobacillus delbrueckii ssp. indicus*.** *Lactobacillus delbrueckii ssp. indicus* was isolated from dahi, a fermented dairy product from India (Dellaglio et al., 2005). It metabolizes sucrose, fructose, lactose, and mannose, but is unable to ferment maltose and trehalose.

***Lacticaseibacillus paracasei ssp. tolerans*.** *Lacticaseibacillus paracasei ssp. tolerans* has not been com-

monly isolated from cheese, probably because it is able to use much fewer carbohydrates than *Lcb. casei* and *Lcb. paracasei* (Minervini and Calasso, 2020).

***Limosilactobacillus reuteri*.** *Limosilactobacillus reuteri* species stably inhabit the gastrointestinal tract of mammals and in some species of birds. In rodents, pigs, and chickens, *Lim. reuteri* is one of the dominant species and colonizes the surfaces of the stratified squamous epithelial lining of the proximal regions of the digestive tract, whereas in humans the ecology of *Lim. reuteri* is less clear (Oh et al., 2010). *Limosilactobacillus reuteri* is found in fermented and probiotic foods and it produces β -hydroxypropionaldehyde (reuterin) during anaerobic metabolism of glycerol. Reuterin is an antimicrobial compound, and there is proposed use of *Lim. reuteri* as a bioprotective culture to control pathogenic microorganisms in dairy products due to the potentially inhibitory concentrations of reuterin achieved in situ (Langa et al., 2013).

***Lentilactobacillus hilgardii*.** *Lentilactobacillus hilgardii* has been found as a minor component in the microbiota of some cheeses along with other lactobacilli such as *Lentilactobacillus diolivorans* (both heterofermentative lactobacilli) as well as homofermentative lactobacilli such as *Schleiferilactobacillus perolens*, *Schleiferilactobacillus harbinensis*, *Lactiplantibacillus fabifermentans*, and *Loigolactobacillus coryniformis* (Gobbetti et al., 2018).

***Loigolactobacillus coryniformis*.** The name of the genus *Loigolactobacillus* relates to its spoilage potential of foods (Zheng et al., 2020). *Loigolactobacillus coryniformis* is usually associated with fermented vegetable products and silage and has been found in cheese as well, such as from an artisanal goat's milk cheese (Martín et al., 2005). Traditionally fermented foods typically have a diverse and complex microbiota and there is interest in isolating wild strains for use as starter cultures in food fermentation, or if they produce antimicrobial compounds (such as some strains of *Lo. coryniformis*) for use as a biopreservative or probiotic culture (Martín et al., 2005).

***Paucilactobacillus wasatchensis*.** The genus *Paucilactobacillus* includes lactobacilli that ferment few carbohydrates (Zheng et al., 2020). Growth is observed at 30 and 37°C but not at 45°C. For *Pa. wasatchensis* the highest level of fermentation is observed with ribose (Ortakci et al., 2015a; Oberge et al., 2016) and gluconate (Oberge et al., 2021) with less growth occurring with galactose, fructose, and *N*-acetylglucosamine (Oberge et al., 2016; McMahon et al., 2020). *Paucilactobacillus wasatchensis* has been isolated from spoiled Cheddar cheese and has been associated with unwanted gas production during cheese storage (Ortakci et al., 2015b,c).

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