

Utilisation de *Weissella* comme starters

Les espèces du genre *Weissella*, plus précisément *W. cibaria*, *W. confusa*, *W. paramesenteroides*, *W. koreensis* et *W. hellenica*, malgré le fait qu'elles soient retrouvées dans plusieurs types d'aliments fermentés, restent encore très peu étudiées et ne sont pas utilisées en tant que starters commerciaux, contrairement aux espèces *Lb. plantarum*, *Lb. delbrueckii*, *Lc. mesenteroides*, *L. lactis*, *Sc. thermophilus* ou *Pc. acidilactici*, entre autres. La caractérisation de ces espèces est l'un des objectifs de ce projet de thèse. Ce chapitre apporte une synthèse bibliographique du genre *Weissella*, des caractéristiques connues et des études des espèces de ce genre. Il est présenté sous la forme d'une revue publiée dans le journal *Fermentation*, intitulée *Why are Weissella spp. not used as commercial starter cultures for food fermentation?*

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Revue : Why are *Weissella* spp. not used as commercial starter cultures for food fermentation



Review

Why Are *Weissella* spp. Not Used as Commercial Starter Cultures for Food Fermentation?

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Abstract: Among other fermentation processes, lactic acid fermentation is a valuable process which enhances the safety, nutritional and sensory properties of food. The use of starters is recommended compared to spontaneous fermentation, from a safety point of view but also to ensure a better control of product functional and sensory properties. Starters are used for dairy products, sourdough, wine, meat, sauerkraut and homemade foods and beverages from dairy or vegetal origin. Among lactic acid bacteria, *Lactobacillus*, *Lactococcus*, *Leuconostoc*, *Streptococcus* and *Pediococcus* are the majors genera used as starters whereas *Weissella* is not. *Weissella* spp. are frequently isolated from spontaneous fermented foods and participate to the characteristics of the fermented product. They possess a large set of functional and technological properties, which can enhance safety, nutritional and sensory characteristics of food. Particularly, *Weissella cibaria* and *Weissella confusa* have been described as high producers of exo-polysaccharides, which exhibit texturizing properties. Numerous bacteriocins have been purified from *Weissella hellenica* strains and may be used as bio-preservative. Some *Weissella* strains are able to decarboxylate polymeric phenolic compounds resulting in a better bioavailability. Other *Weissella* strains showed resistance to low pH and bile salts and were isolated from healthy human feces, suggesting their potential as probiotics. Despite all these features, the use of *Weissella* spp. as commercial starters remained non-investigated. Potential biogenic amine production, antibiotic resistance pattern or infection hazard partly explains this neglecting. Besides, *Weissella* spp. are not recognized as GRAS (Generally Recognized As Safe). However, *Weissella* spp. are potential powerful starters for food fermentation as well as *Lactococcus*, *Leuconostoc* or *Lactobacillus* species.

Keywords: *Weissella*; food fermentation; starter culture

1. Introduction

Fermentation has been applied for thousand years as a method to preserve perishable foods. It seems that fermentation appeared in the period 8000–6000 BC in Iraq with the fabrication of cheese. Later, in the period 4000–2000 BC, Egyptians discovered how to use yeasts to make leavened bread and wine [1]. Nowadays, a large variety of fermented foods are consumed around the world and appreciated for their organoleptic and sensory properties, including cheese, yoghurt, kefir, beer, *Kombucha*, *Pozol*, sourdough, *Kimchi*, olives, sauerkraut, pickles, *Tempe*, *Gari*, *Fufu* or sausages [2]. Whatever the nature of the raw material, fermented foods are obtained either by spontaneous fermentation or by the use of starter cultures. Spontaneous fermentation results from the combined actions of microorganisms originating from the raw materials or the environment, including yeast, fungi and bacteria [3]. Started fermentation consists in inoculating the raw material with a single or a mix of safe microbial strains in order to control and accelerate the fermentation process. These two different processes result in different molecular changes and different sensory properties.

Microorganisms used in commercial starter cultures include bacteria, yeasts and molds. Molds are used in the production of meat and cheese products and the species available as commercial starter cultures are *Penicillium roqueforti*, *Penicillium nalgiovense* and *Penicillium chrysogenum* [4]. Yeasts are used in the production of beer, wine, bread and cheese. The species available as commercial starter cultures include *Debaryomyces hansenii*, *Galactomyces geotrichum* but mostly *Saccharomyces cerevisiae*. Among the microorganisms available as starter cultures, lactic acid bacteria (LAB) are the most diverse. They are used to start wine, bread, vegetables, meat and dairy product fermentation.

LAB are a group of gram-positive bacteria, non-spore forming, cocci or rods, that produce lactic acid as the major end-product of carbohydrate fermentation. LAB are extensively involved in spontaneous fermentation and the major genera are *Carnobacterium*, *Enterococcus*, *Lactobacillus*, *Lactococcus*, *Leuconostoc*, *Oenococcus*, *Pediococcus*, *Streptococcus*, *Tetragenococcus*, *Vagococcus* and *Weissella* [5]. They play a central role in the fermentation process. Particularly, they cause a rapid acidification of the raw material by the production of lactic acid and produce several other important compounds such as ethanol, carbon dioxide, bacteriocins, exopolysaccharides (EPS), aromatic compounds, vitamins or useful enzymes. Lactic fermented foods have a long and safe history of consumption and have been associated with health benefits, safety, nutritional and sensory properties improvement. For these reasons, LAB have gained interest these last decades and the research for new LAB starters is increasingly developed.

Nowadays, more than 20 LAB species are available as commercial starter cultures. Among those, *Lactobacillus plantarum*, *Lb. delbrueckii*, *Lb. sakei*, *Lactococcus lactis*, *Streptococcus thermophilus*, *Pediococcus pentosaceus* and *Leuconostoc mesenteroides* are the species mostly used [6–8]. They have been used for decades in food fermentation, are recognized as safe and were selected from technological and sensorial assays.

Over the past 20 years, scientists have gained interest for the genus *Weissella*. *Weissella* was proposed as a genus in 1993 from re-classified *Lactobacillus* and *Leuconostoc* spp. They are frequently detected in many fermented foods [9–13] and participate to the final stage of the fermented product, together with *Lactobacillus* and *Leuconostoc*. As other LAB species used as commercial starters, *Weissella* spp. produce bacteriocins, EPS and hydrolytic enzymes [14]. However, they are still not used as commercial starters in food industries and remain under a laboratory investigation stage.

This review aims to understand the reasons why *Weissella* spp. are not used as commercial starters in food fermentation. Taxonomy, characteristics and the role of *Weissella* spp. in spontaneous fermentation were investigated, as well as their functional and technological properties, and possible reasons that would explain the poor investigation of *Weissella* spp. as starters.

2. *Weissella* Genus

2.1. Phenotypic and Genetic Characteristics of *Weissella* spp.

Weissella genus belongs to the *Leuconostocaceae* family together with the genera *Leuconostoc*, *Oenococcus* and *Fructobacillus* [15]. *Weissella* genus was proposed in 1993 from previously *Leuconostoc* and *Lactobacillus* classified species. *Weissella* spp. are gram-positive, catalase negative, asporogenous, non-motile, except for *W. beninensis*, and lack cytochrome [16]. Cells are either short rods or ovoid and occur in pair or in short chains. They are facultative anaerobic with an obligatory fermentative metabolism. *Weissella* spp. are hetero-fermentative: glucose is fermented via the hexose-monophosphate and phosphoketolase pathways. End products are lactic acid, CO₂, ethanol and acetic acid, except for *Weissella ceti* which does not produce gas [17]. Configuration of lactic acid can be either D(-) or DL. Hydrolysis of arginine depends on the species whereas all *Leuconostoc* spp. are arginine-negative. Cell-wall peptidoglycan is composed of lysine and the interpeptide bridge contains alanine or serine, except for *Weissella kandleri* which contains glycine. Growth mainly occurs between 15 °C and 37 °C, but some strains of *Weissella cibaria* and *Weissella confusa* are able to grow at 45 °C. The type

species is *Weissella viridescens*. Fusco et al. [18] have drawn a complete description of *Weissella* spp., except for *Weissella bombi* and *Weissella jogaejeotgali* which have been described afterwards.

Distinction between *Weissella*, *Leuconostoc* and heterofermentative lactobacilli remains impossible based only on morphological observation. Since they produce gas from carbohydrates, members of the genus *Weissella* may be distinguished from homofermentative lactobacilli, enterococci, pediococci, lactococci and streptococci. Generally, identification of *Weissella* spp. is performed with molecular methods, such as 16S rRNA gene sequencing, amplified ribosomal DNA restriction analysis (ARDRA), ribotyping, Matrix-associated laser desorption ionization Time-of-Flight (MALDI-ToF), repetitive element-PCR fingerprinting using (GTG)₅-PCR or fluorescent-Amplified Fragment Length Polymorphism (fAFLP) [18].

The genome sequence of 28 strains belonging to 12 species has been published (GenBank). The smallest genomes belong to *Weissella halotolerans* (1.36 Mb) and *W. ceti* (1.35 to 1.39 Mb), which share the same taxonomic branch. The largest genomes belong to *W. cibaria* (2.32 to 2.47 Mb), *W. confusa* (2.18 to 2.28 Mb), *W. jogaejeotgali* (2.11 Mb) and *Weissella oryzae* (2.13 Mb), all these four species having been isolated from fermented foods. The core-proteome of *Weissella* represented 729 COGs (Clusters of Orthologous Genes), over a pan-proteome of 4712 COGs. Core-proteome is essentially involved in housekeeping but shows a relative lack of shared traits between all species, which might explain the diversity of niches of the species.

2.2. Taxonomical Position and Specific Traits

Collins et al. [19] demonstrated that *Lactobacillus confusus*, *Lactobacillus kandleri*, *Lactobacillus minor*, *Lactobacillus viridescens* and *Lactobacillus halotolerans* were phylogenetically related to *Leuconostoc paramesenteroides*. Besides, a unique murein type, Lys-Ser/Ala, was reported within *Lb. viridescens*, *Lb. minor* and *Lb. halotolerans*, which was identical to that found in the *Lc. paramesenteroides* group [20]. Hence, from this group, the genus *Weissella* was created and species were named *Weissella paramesenteroides*, *W. confusa*, *W. kandleri*, *Weissella minor*, *W. viridescens*, *W. halotolerans* plus *Weissella hellenica*, isolated from fermented sausages [19]. Based on 16S and 23S rRNA sequence analyses, three evolutionary lines were distinguished in *Leuconostoc* spp., nowadays named *Leuconostoc sensu stricto*, *W. paramesenteroides* and *Oenococcus oeni* [21]. The genera *Oenococcus* and *Fructobacillus* have been proposed from re-classified *Leuconostoc* spp. [22,23], but interestingly, *Weissella* was the only genus of the *Leuconostocaceae* family gathering re-classified *Leuconostoc* and *Lactobacillus* spp. Currently, the genus *Weissella* comprises 21 species, isolated from a high variety of sources (Table 1). Based on partial 16S rRNA coding sequence, several branches can be separated within *Weissella* spp. (Figure 1 and Table 1). *Weissella ghanensis*, *Weissella fabaria*, *Weissella fabalis*, all isolated from fermented cassava, and *W. beninensis* belong to the same branch. *W. ceti*, *W. halotolerans*, *W. minor*, *Weissella uvarum* and *W. viridescens* share another taxonomic branch, which mainly originates from previous *Lactobacillus* spp. [20]. Species of this branch harbor diverse habitats. *W. viridescens* and *W. halotolerans* have been isolated from meat products [20,24], *W. minor* from milking machine sludge [20], *W. ceti* from a beaked whale [17] and *W. uvarum* from wine grapes [25].

Weissella diestrammenae, *W. kandleri* and *Weissella koreensis* constitute a third branch with strains from different sources. *W. kandleri* and *W. koreensis* were isolated from *Koumiss*, a fermented drink from mare milk, and from kimchi, respectively. *W. cibaria* and *W. confusa* belong to the same branch and share numerous habitats. Both species have been found in fermented foods, animal, clinical samples and human feces. These two species are hardly distinguishable since they share 99.6% of identity in their 16S rRNA coding sequence. Another branch comprises *W. bombi*, *W. hellenica*, *W. jogaejeotgali*, *W. paramesenteroides* and *Weissella thailandensis*. All the species from this branch have been isolated from fermented foods except *W. bombi* isolated from insect gut. Interestingly, *W. jogaejeotgali* and *W. thailandensis* are closely related and both have been detected in *Jeotgal*, a fermented seafood product. *W. paramesenteroides* and *W. hellenica* were detected in fermented sausages, fermented milk or cheese.

Table 1. *Weissella* species, sources, taxonomic branch and genome size.

<i>Weissella</i> spp.	Sources	Genome Size (Mb)	Taxonomic Branch	References
<i>W. fabalis</i>	Cocoa bean fermentation	-	1	[26]
<i>W. fabaria</i>	Cocoa bean fermentation	-	1	[27]
<i>W. ghanensis</i>	Cocoa bean fermentation	-	1	[28]
<i>W. beninensis</i>	Fermented cassava	-	1	[16]
<i>W. jogaejeotgali</i>	Jeotgal (fermented seafood)	2.11 (CP014332.1)	2	[29]
<i>W. thailandensis</i>	Jeotgal, Mexican cheese, Thai fermented meat and fish	1.97 (HE575133 to HE575182)	2	[30]; See Table 2
<i>W. paramesenteroides</i>	Fermented sausages, fermented fruits and vegetables, fermented milk, cheese, fermented cassava, sourdough, fermented cereal, fermented fish	1.96 (NZ_ACKU00000000.1)	2	[31,32]; See Table 2
<i>W. hellenica</i>	Fermented sausages, fermented vegetables, fermented milk, cheese, fermented maize beverage, fermented meat	1.82–1.92 (NZ_BBK00000000.1; NZ_FMAW00000000.1)	2	[19]; See Table 2
<i>W. bombi</i>	Gut of a bumble bee	-	2	[33]
<i>W. halotolerans</i>	Meat products, fermented sea food, cheese, fermented sausages	1.36 (NZ_ATUU00000000.1)	3	[20]; See Table 2
<i>W. ceti</i>	Beaked whale	1.35–1.39 (NZ_ANCA00000000.1; NZ_CP009224.1)	3	[17]
<i>W. viridescens</i>	Meat products, dry salami, kimchi, fermented milk, cheese, fermented cereal beverage, fermented sausages, fermented fish	1.53–1.56 (NZ_JQBM00000000.1; NZ_CYXF00000000.1)	3	[24]; See Table 2
<i>W. minor</i>	Sludge of milking machine, fermented fruits and vegetables, fermented dry salami	1.77 (NZ_JQCD00000000.1)	3	[20]; See Table 2
<i>W. uvarum</i>	Wine grapes	-	3	[25]
<i>W. diestrammenae</i>	Gut of a camel cricket	-	4	[34]
<i>W. kandleri</i>	Desert spring and desert plants	1.33 (NZ_JQBP00000000.1)	4	[35]
<i>W. koreensis</i>	Kimchi, fermented vegetables	1.42–1.73 (NC_015759.1; NZ_AKGG00000000.1)	4	[36]; See Table 2
<i>W. cibaria</i>	Malaysian ingredients foods, clinical samples, animals, human feces, fermented fruits and vegetables, fermented dairy products, cheese, fermented cassava, fermented cereal foods and beverages, sourdough, cocoa bean fermentation, fermented sausages, fermented fish	2.32–2.47 (NZ_AEKT00000000.1; NZ_CP012873.1)	5	[37]; See Table 2
<i>W. confusa</i>	Sugar cane, animal, clinical samples, Malaysian ingredients foods, human feces, pasta manufacturing, kimchi, fermented vegetables, fermented milk, cheese, fermented cereal foods, fermented cassava, sourdough, cocoa bean fermentation, pork sausages, fermented fish	2.18–2.28 (NZ_MNBZ00000000.1; NZ_CAGH00000000.1)	5	[37,38]; See Table 2
<i>W. oryzae</i>	Fermented rice grains, cereal based beverage	2.13 (NZ_BAWR00000000.1)	0	[34,39]
<i>W. soli</i>	Soil, kimchi, Jeotgal, stinky tofu, leek fermentation, sliced cabbage	-	0	[40]; See Table 2; [31]

Table 2. Detection of *Weissella* spp. in fermented foods.

Food Category	Fermented Product	<i>Weissella</i> Species	Reference
Fruits and Vegetables Fermented Food	Kimchi (mix vegetables)	<i>W. koreensis</i> , <i>W. cibaria</i> , <i>W. confusa</i> , <i>W. soli</i> , <i>W. hellenica</i>	[36,41–46]
	Yan-dong-gua (wax gourd)	<i>W. cibaria</i> , <i>W. paramesenteroides</i>	[47]
	Pobuzihi (cummingcordia)	<i>W. cibaria</i> , <i>W. paramesenteroides</i>	[48]
	Jiang-gua (cucumbers)	<i>W. cibaria</i> , <i>W. hellenica</i>	[49]
	Yan-tsai-shin (broccoli stems)	<i>W. cibaria</i> , <i>W. paramesenteroides</i> , <i>W. minor</i>	[50]
	Yan-Jiang (ginger)	<i>W. cibaria</i>	[51]
	Yan-taozih (pickled peaches)	<i>W. cibaria</i> , <i>W. paramesenteroides</i> , <i>W. minor</i>	[52]
	Xi-gua-mian (watermelon)	<i>W. paramesenteroides</i>	[53]
	Dochi (black beans)	<i>W. paramesenteroides</i>	[54]
	Koozh (cucumber)	<i>W. koreensis</i>	[55]
	Suan-tsai, fu-tsai (mustard product)	<i>W. cibaria</i> , <i>W. paramesenteroides</i>	[56]
	Jeotgal (sea food)	<i>W. thailandensis</i> , <i>W. halotolerans</i> , <i>W. soli</i> , <i>W. cibaria</i> , <i>W. jogaejeotgali</i>	[29,43]
	Stinky tofu	<i>W. cibaria</i> , <i>W. confusa</i> , <i>W. paramesenteroides</i> , <i>W. soli</i>	[57]
	Tuaw jaew (soybeans)	<i>W. confusa</i>	[58]
	Fermented sea food	<i>W. paramesenteroides</i>	[59]
	Fermented cabbage	<i>W. cibaria</i>	[60]
	Tempoyak (durian)	<i>W. paramesenteroides</i>	[61]
	Commercial cucumber fermentation	<i>W. cibaria</i> , <i>W. paramesenteroides</i>	[62]
	Cauliflower and mixed vegetables	<i>W. cibaria</i> , <i>W. paramesenteroides</i>	[63]
	Well-fermented leek kimchi	<i>W. viridescens</i> , <i>W. confusa</i> , <i>W. cibaria</i>	[64]
Leek fermentation	<i>W. soli</i> , <i>Weissella</i> spp.	[65]	
Commercial sauerkraut	<i>Weissella</i> spp.	[66]	
Sauerkraut	<i>Weissella confusa/cibaria</i>	[67]	
Dairy Fermented Food	Nono (Fermented skimmed milk), cheese	<i>W. confusa</i>	[68]
	Nunu (Ghanaian fermented milk)	<i>W. confusa</i>	[69]
	Kule naoto (Masain fermented milk in Kenya)	<i>W. paramesenteroides/Lc mesenteroides</i>	[70]
	Maisian fermented zebu milk	<i>W. confusa (Lb confusus)</i> , <i>W. viridescens (Lb viridescens)</i>	[71]
	Mongolian fermented milk	<i>W. viridescens</i>	[72]
	Shubat (fermented camel milk)	<i>W. hellenica</i>	[73]
	Dahi (Indian yogurt like product)	<i>W. cibaria</i>	[60]
	Italian cheese	<i>W. confusa</i> , <i>W. cibaria</i>	[74]
	Mexican cheese (Cotija cheese)	<i>W. thailandensis</i>	[75]
	Manura (hard cheese)	<i>W. paramesenteroides</i> , <i>W. viridescens</i>	[76]
	Scamorza Altamura Cheese	<i>W. viridescens</i>	[77]
	Mozarella cheese	<i>W. hellenica</i>	[78]
	Cheddar cheese	<i>W. halotolerans</i> , <i>W. viridescens</i>	[79]
Romanian cheese	<i>W. viridescens</i>	[80]	
Mongolian dairy products	<i>W. cibaria</i>	[81]	

Table 2. Cont.

Food Category	Fermented Product	Weissella Species	Reference
Starchy or Cereal-Based Fermented Food and Diverse	Togwa (sorghum based food)	<i>W. confusa</i>	[82]
	Gari, Attieke, Lafun (cassava)	<i>W. paramesenteroides</i> , <i>W. cibaria</i> , <i>W. confusa</i> , <i>W. beninensis</i>	[16,83–86]
	Idli batter (Indian fermented rice and black gram based food)	<i>W. confusa</i> , <i>W. cibaria</i>	[60,87]
	French wheat sourdough, buckwheat and teff sourdough, Italian sourdough, Turkish sourdough, spontaneous sourdough	<i>W. confusa</i> , <i>W. cibaria</i> , <i>W. paramesenteroides</i>	[10,88–93]
	Mexican <i>Pozol</i>	<i>W. paramesenteroides</i>	[94]
	Fermented rice grains	<i>W. oryzae</i>	[95]
	Chicha (maize based beverage)	<i>W. confusa</i> , <i>W. hellenica</i> , <i>W. paramesenteroides</i>	[96]
	Kunu-zaki (Nigerian cereal based food)	<i>W. confusa</i>	[97]
	Boza (Bulgarian cereal-based beverage)	<i>W. confusa</i> , <i>W. oryzae</i>	[39]
	Fura (African millet based food)	<i>W. confusa</i>	[98]
	Borde (Ethiopian cereal beverage)	<i>W. confusa</i> , <i>W. viridescens</i>	[99]
	Cocoa bean fermentation	<i>W. cibaria</i> , <i>W. ghanensis</i> , <i>W. confusa</i> , <i>W. paramesenteroides</i> , <i>W. fabaria</i> , <i>W. fabalis</i>	[26–28,100]
	Makgeolli (Korean starchy alcoholic beverage)	<i>W. confusa</i> , <i>W. cibaria</i> , <i>W. paramesenteroides</i>	[101]
Fermented Meat and Fish Product	Nham (Thai fermented pork sausage)	<i>W. cibaria</i> , <i>W. confusa</i>	[102–104]
	Italian fermented sausages	<i>W. hellenica</i> , <i>W. paramesenteroides</i>	[105,106]
	Greek dry-fermented sausages	<i>W. viridescens</i>	[107]
	Fermented sausages in Hungary	<i>W. paramesenteroides</i> / <i>W. hellenica</i> , <i>W. viridescens</i>	[108]
	Alheira (Fermented sausage in Portugal)	<i>W. cibaria</i> , <i>W. viridescens</i>	[109]
	Sucuk (fermented turkish sausages)	<i>W. viridescens</i>	[110]
	Portuguese fermented sausage	<i>W. halotolerans</i>	[111]
	Smoked horsemeat sausage	<i>W. hellenica</i> , <i>Weissella</i> spp.	[112]
	Fermented sausages	<i>W. hellenica</i>	[19]
	Fermented Greek dry salami	<i>W. hellenica</i> , <i>W. viridescens</i> , <i>W. paramesenteroides</i> , <i>W. minor</i> , <i>W. halotolerans</i>	[113]
	Chinese dong fermented meat	<i>W. hellenica</i>	[114]
	Mum (Thai fermented meat)	<i>W. thailandensis</i>	[58]
	Pla-ra, Pla-ra sub, plaa-som, pla-jom, pla-jaw (Thai fermented fish)	<i>W. thailandensis</i> , <i>W. cibaria</i> , <i>W. confusa</i> , <i>W. paramesenteroides</i> , <i>W. viridescens</i>	[30,58,115–117]
Sidra (Fish products)	<i>W. confusa</i>	[118]	

Finally, two species remained unclassified, *W. soli* and its closest neighbor species, *W. oryzae*. *W. soli* is the only *Weissella* spp. which has been isolated from soil and *W. oryzae* has been isolated from fermented rice grains.

All *Weissella* species except five were isolated from fermented food (Table 1).

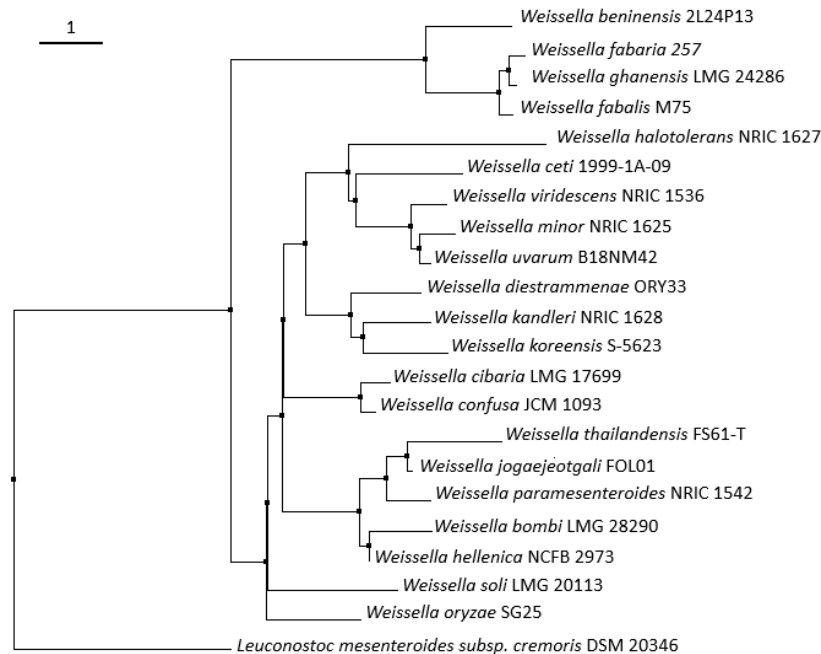


Figure 1. Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences of *Weissella* and the related species *Leuconostoc mesenteroides* obtained from Clustal W2 Multiple Sequence Alignment. The relative genetic distances are indicated by the scale bar and the branch lengths. *Weissella* species Accession numbers: *W. beninensis* 2L24P13; EU439435. *W. fabaria* 257; FM179678. *W. ghanensis* LMG 24286; AM882997. *W. fabalis* M75; HE576795. *W. halotolerans* NRIC 1627; AB022926. *W. ceti* 1999-1A-09; FN813251. *W. viridescens* NRIC 1536; AB023236. *W. minor* NRIC 1625; NR_040809. *W. uvarum* B18NM42; KF999666. *W. diestrammenae* ORY33; JQ646523. *W. kandleri* NRIC 1628; AB022922. *W. koreensis* S-5623; AY035891. *W. cibaria* LMG 17699; AJ295989. *W. confusa* JCM 1093; AB023241. *W. thailandensis* FS61-T; AB023838. *W. jogaejeotgali* FOL01; NR_145896. *W. paramesenteroides* NRIC 1542; AB023238. *W. bombi* LMG 28290; LK054487. *W. hellenica* NCFB 2973; X95981. *W. soli* LMG 20113; AY028260. *W. oryzae* SG25; AB690345.

3. Occurrence of *Weissella* in Spontaneous Fermentation

3.1. General Occurrence

Numerous *Weissella* strains have been isolated from a large panel of spontaneous fermented foods including fruits and vegetables-based foods, fermented meat and fish products and starchy or cereal-based foods (Table 2). A frequent detection of *Weissella* spp. in a large variety of spontaneous fermented foods strengthens the fact that they are able to adapt to a multitude of environment and play an important role in the fermentation process. Moreover, the identification of *Weissella* spp., which dominates the microflora of fermented foods, is an important step for the development of new starter cultures for the fermentation industry. These are the reasons why we hypothesized that the high presence and the role of *Weissella* spp. in fermented food justifies to pay attention to a possible use as starter in the food fermentation industry.

3.2. Fruits and Vegetables-Based Products

W. cibaria, *W. confusa* and *W. paramesenteroides* have been isolated from fermented leek, fermented cabbage, fermented cauliflower and sauerkraut [63,65,67,119]. These species but also *W. soli*, *W. thailandensis*, *W. hellenica*, *W. koreensis*, *W. minor*, *W. halotolerans* and *W. jogaejeotgali* have been isolated from Asian traditional fruits and vegetables-based fermented products, like *Kimchi*, *Yan-dong-gua*, *Pobuzih*, *Jiang-gua*, *Yan-tsai-shin*, *Yan-jiang*, *Yan-taozih*, *Xi-gua-mian*, *Dochi*, *Suan-tsai*, *Jeotgal* and Stinky tofu (Table 2) [29,36,41–44,46–54,56,57]. *Kimchi* is a Korean traditional fermented vegetable composed of Chinese cabbage and other ingredients like radish, green onion, red pepper powder, garlic, ginger and fermented seafood (*Jeotgal*) [120]. *Yan-taozih* (pickled peaches), *Xi-gua-mian* (fermented watermelon) and *Pobuzih* (fermented cummingcordia) are popular fermented fruits in China and Taiwan [53,120]. *Yan-dong-gua*, *Jiang-gua*, *Yan-tsai-shin* and *Yan-jiang* are traditional fermented foods of Taiwan, composed of fermented wax gourd, cucumber, broccoli stems and ginger, respectively.

Interestingly, *Weissella* spp. are frequently found in vegetables which belong to the cabbage family (cabbage, broccoli, cauliflower and radish) and in fruits from the gourd family (cucumbers, wax gourd, watermelon). Nowadays, cabbages, cucumbers and olives are the main vegetables industrially transformed by lactic acid fermentation [7]. Persistence of *Weissella* spp. in cabbage and gourd-based fermented products is a cornerstone for its use as starters for these kinds of products.

Actually, the role of *Weissella* spp. in vegetable fermentation is not clearly understood. They are frequently isolated from fermented vegetables and participate to the final stage of the fermented product. *W. cibaria* and *W. paramesenteroides* are responsible for the fermentation of *Yan-dong-gua*. Surprisingly, *W. cibaria* was replaced by *W. paramesenteroides* after 5 days of fermentation. In addition, after 28 days of fermentation, both *Weissella* species disappeared [47]. These species disappearances remain not understood and need to be investigated. Interestingly, these two species occur together in other fermented foods and similar changes were observed. Both species were detected in the 3-days initial fermentation of *Fu-tsai* and spontaneous cauliflower and mixed-vegetables fermentation but disappeared during the following steps of the fermentation processes [56,63]. These two species seem to work together in vegetables fermentation and constitute an interesting option for their use as a mixed starter culture. *W. cibaria*, *W. confusa* and *W. koreensis* are frequently involved in *Kimchi* fermentation. *W. confusa* (together with *Lc. citreum*) was present throughout the fermentation process of kimchi, suggesting its importance during the fermentation [46]. *W. cibaria* and *W. confusa* have been detected in the early stage of kimchi fermentation, but were replaced by *Lb. plantarum*, *Lb. brevis* and *Lc. pseudomesenteroides*. It seemed that *W. cibaria* and *W. confusa* started the fermentation and created an environment suitable for the growth of *Lactobacillus* spp. [11]. It has been shown that *W. soli* was present during the early stage of fermentation of kimchi but was replaced by *W. koreensis* [42]. Because kimchi is generally processed by spontaneous fermentation, the LAB microflora of kimchi may vary. However, the LAB species most frequently found in kimchi are *Lc. citreum*, *Lc. mesenteroides*, *Lc. lactis*, *W. cibaria*, *W. confusa*, *W. koreensis*, *Lb. plantarum* and *Lb. brevis*. Generally, in vegetable fermentation, *Weissella* and *Leuconostoc* spp. start the fermentation and are followed by more acidic tolerant species such as *Lactobacillus* spp.

3.3. Dairy Fermented Foods

W. confusa, *W. cibaria*, *W. thailandensis*, *W. paramesenteroides*, *W. hellenica* and *W. viridescens* have been detected in different types of cheese and fermented milk (Table 2) [68–81].

W. paramesenteroides represented a high proportion of LAB isolated both from the surface and interior of fresh *Manura* cheese [76]. Besides, it was also one of the predominant LAB species isolated during cheese ripening, suggesting its important role in the production of *Manura* cheese. *W. confusa* appeared occasionally in *Nunu* fermented milk [69]. *W. confusa* NGB-82 (*Lb. confusus*) together with *L. lactis* subsp. *lactis* MOS-11 dominated in *Masai* fermented zebu milk. These two strains were used as starter cultures for this kind of milk and were able to rapidly acidify the media and inhibit the growth of *S. aureus* and *E. coli* [71]. However, *W. confusa* was not present in another *Masian* fermented milk [70].

W. viridescens was occasionally found in *Scamorza Altamura* cheese [77] and in Romanian dairy products [80]. *W. hellenica* 1M30 was able to decrease the pH of skimmed milk for the production of *Mozarella* cheese and showed a proteolytic activity on milk proteins [78]. This strain may be a suitable starter culture for industrial processing of *Mozarella* cheese. This was not the case for fermented camel milk since *W. hellenica* was found in only one sample suggesting a contamination [73].

3.4. Meat and Fish-Based Products

The main *Weissella* species involved in meat and fish fermentation are *W. cibaria*, *W. confusa*, *W. paramesenteroides*, *W. hellenica*, *W. viridescens* and in a lesser part, *W. thailandensis* (Table 2). *W. thailandensis* has been first isolated from *Pla-ra*, a fermented fish product from Thailand [30] and more recently, in *Mum*, a Thai fermented meat product [86]. Miyashita et al. [86] isolated also *W. cibaria*, *W. confusa*, *W. paramesenteroides* and *W. viridescens* in several other Thai fermented fish products like, *Pla-ra sub*, *Plaa-som*, *Pla-jom* and *Pla-jaw*. Presence of *W. cibaria* and *W. confusa* in *Plaa-som* was confirmed by [115,116]. *W. cibaria* dominated the early stage of fermentation and contributed to the product finishing.

The main LAB involved in dry and fermented sausages are *Lb. plantarum*, *Lb. sakei* and *Lb. curvatus*. However, *W. cibaria*, *W. paramesenteroides*, *W. hellenica* and *W. viridescens* are frequently detected in fermented sausages [102,105–109,113]. *W. hellenica* represented a low portion of the LAB isolated from Italian sausages, suggesting that its contribution to the fermentation process was not really important. This observation was confirmed by [107] as *W. viridescens* has been occasionally detected in Greek-dry fermented sausages. *W. minor* has been detected in Greek-fermented sausages but should not be used as starter for meat fermentation due to its high production of gas and peroxide [113]. As a whole, generally, *Weissella* spp. represent a minority part of LAB involved in fermented sausages and their use as starter cultures for fermented meat products is almost not considered.

3.5. Starchy and Cereal-Based Products

As shown in Table 2, *W. confusa* has been detected in several cereal-based fermented foods like *Togwa*, *Kunu-zaki*, *Boza*, *Fura* and *Borde* [39,82,97–99]. *W. cibaria*, *W. confusa* and *W. paramesenteroides* have been found in several fermented cassava products, such as *Gari*, *Attieke* and *Lafun* [16,83–86]. These species have also been isolated from different types of sourdough [10,88–90,92].

In *Togwa* fermentation, *W. confusa* was present from the beginning to the end of the fermentation, together with *Lb. plantarum*, *Lb. brevis*, *Lb. fermentum*, *Lb. cellobiosus* and *P. pentosaceus*. However, *Lb. plantarum* was the dominant species [82]. *W. confusa* has been shown to be the dominant species together with *Lb. fermentum* during the fermentation of *Fura*. Indeed, these two species were isolated from eight different processing sites and at almost all fermentation stages [98]. *W. confusa* and *W. viridescens* were the dominant species during the fermentation of *Borde*, together with *Lb. brevis* and *P. pentosaceus*. These two species are thus adapted to the niche of *Borde* fermentation and constitute potential starter cultures for the industrial production of *Borde* [99]. *W. confusa* together with *Lb. plantarum* and *Lb. fermentum* were also the dominant species during the fermentation of *Lafun* [86].

4. Spontaneous Versus Started Fermentation

4.1. Role of Starters in Food Fermentation

Traditional fermented foods are mainly obtained by a naturally occurred fermentation, resulting from competitive activities of different microorganisms derived from the raw material or the environment, including yeast, fungi and lactic acid bacteria [3,121]. Some traditional fermented foods have been consumed for centuries and remained today an important part of the human diet. Some famous ancient fermented foods are kefir, sauerkraut, *Kimchi*, *kombucha* and wine. Kefir, a fermented milk beverage, is a drink originated from the Caucasian mountains and represents today a market of €78.7 million only in North America [122]. Over spontaneous fermentation, microorganisms

that are best adapted to the environment and exhibit the highest growth rate, dominate the fermentation process [123]. Generally, a succession of flora is observed [7,124]. Due to multiple microorganisms' activities, spontaneous fermentation remains difficult to control. Thus, the quality of a spontaneous fermented product is not predictable, undesirable change of the sensory profile can occur and the risk of fermentation failure can be important [7]. Using starter culture is the most efficient way to control the fermentation process, to ensure quality and safety of the fermented product. A starter culture can be defined as a microbial preparation containing a high number of at least one microorganism to produce a fermented food by accelerating its fermentation process and bring desirable sensory properties [8,121]. In 1873, Lister isolated the first pure bacterial culture, *Bacterium lactis* (nowadays *Lactococcus lactis*) which became, in 1890, the first starter culture to be used for the cheese and sour-milk production [121]. Nowadays, a number of LAB starters is used in the food industry (Table 3), producing a high diversity of fermented products. The majority of LAB starters belong to the genera *Lactobacillus*, *Lactococcus*, *Streptococcus*, *Pediococcus*, *Leuconostoc* and *Bifidobacterium*. *Lactobacillus* species are used for the production of dairy, vegetable, cereal and meat products. *Lactococcus* species are mainly used for dairy products and the main species used as commercial starter is *L. lactis*. *Streptococcus thermophilus* is the only species within the genus *Streptococcus* to be used as commercial starter. It is used for the production of yoghurt and some cheeses, due to its particular rapid acidification in milk fermentation [125]. Among the *Leuconostoc* spp., *Lc. mesenteroides* is the main species used as commercial starter. *Lc. mesenteroides* is used for the production of buttermilk and some cheese [126]. *Pediococcus* species are mainly involved in the fermentation of meat products and of sourdough. *P. pentosaceus* and *P. acidilactici*, together with *Lb. sakei*, *Lb. curvatus*, *Lb. plantarum*, *Lb. pentosus* and *Lb. casei* are the species mostly used as commercial starter for meat products [124]. *Oenococcus oeni*, *Lb. plantarum* and *Lb. hilgardii* are available as commercial starter cultures for the malolactic fermentation of wine since the beginning of the 1980s [3].

Before commercialization, starters have to pass many steps of selection and performance tests.

4.2. Expected Characteristics of Starters

General criteria for the selection of starters deal with safety, technological and economical aspects [3]. The starter culture should be able to develop some expected flavor and aroma, to improve safety, nutritional and shelf-life properties of foods. Thus, criteria for selection of starters are mainly divided in four aspects: technological, sensory, nutritional and safety (Table 4). A quick growth and a high acidification rate are the first criteria for the selection of starter. A rapid acidification will create a safe environment at the initial stage of the fermentation and thus reduce food pathogen hazard and spoilage probability. During fermentation, LAB can be exposed to salt stress due to important amounts of added salt, but also in fruits to high sugar levels. Therefore, adaptation to hyperosmotic environments has to be considered, especially for making fruits, vegetables or meat based products.

The synthesis of antimicrobial compounds or bacteriocins is desired during fermentation, as these compounds inhibit the proliferation of pathogens or spoilage microorganisms. Bacteriocins are natural antimicrobial proteins produced by bacteria, including LAB, and their use in food industries in an interesting alternative for food preservation. Nisin, a bacteriocin produced by several *L. lactis* strains is commercially available in UE as a bio-preservative [127]. Lactic acid, acetic acid, ethanol, hydrogen peroxide (H₂O₂), diacetyl, reuterin and bacteriocins are produced by LAB and show inhibiting activities against food borne pathogens, including both gram-negative and gram-positive bacteria [128]. In addition, LAB are able to produce antifungal compounds which inhibit mycotoxin producer growth and can bind and reduce the content of mycotoxins [129].

Table 3. Lactic acid bacteria used as commercial starters in the food industry.

Type of Fermented Product	Product	LAB Species Used as Commercial Starters	References
Dairy Fermented Foods	Yoghurt	<i>S. thermophilus</i> , <i>Lb. delbruecki</i> subsp. <i>bulgaricus</i>	[130]
	Fermented/Probiotic milk	<i>Lb. casei</i> , <i>Lb. acidophilus</i> , <i>Lb. rhamnosus</i> , <i>Lb. johnsonii</i> , <i>B. lactis</i> , <i>B. bifidum</i> , <i>B. brevis</i>	
	Kefir	<i>Lb. kefir</i> , <i>Lb. kefiranofacies</i> , <i>Lb. brevis</i>	
	Butter and buttermilk	<i>L. lactis</i> subsp. <i>lactis</i> , <i>L. lactis</i> subsp. <i>diacetylactis</i> , <i>L. lactis</i> subsp. <i>cremoris</i> , <i>Lc. mesenteroides</i> subsp. <i>cremoris</i>	
	Swiss and Italian type cheeses	<i>Lb. delbrueckii</i> subsp. <i>lactis</i> , <i>Lb. helveticus</i> , <i>Lb. casei</i> , <i>Lb. delbrueckii</i> subsp. <i>bulgaricus</i> , <i>S. thermophilus</i>	
	Cheeses (with or without eyes)	<i>L. lactis</i> subsp. <i>Lactis</i> , <i>L. lactis</i> subsp. <i>cremoris</i> , <i>L. lactis</i> subsp. <i>diacetylactis</i> , <i>Lc. mesenteroides</i> subsp. <i>cremoris</i>	
Fermented Cereals	Sourdough	<i>Lb. brevis</i> , <i>Lb. plantarum</i> , <i>Lb. sanfranciscensis</i> , <i>Lb. casei</i> , <i>Lb. delbrueckii</i> , <i>Lb. fermentum</i> , <i>P. pentosaceus</i> , <i>P. acidilactic</i> , <i>Lb. pontis</i> , <i>Lb. crispatus</i> , <i>Lb. paracasei</i> , <i>Lb. helveticus</i> , <i>Lb. paralimentarius</i> , <i>Lc. lastis</i>	[6]
Fruits and Vegetables	Sauerkraut	<i>Lc. mesenteroides</i> , <i>Lb. plantarum</i> , <i>P. acidilactici</i>	[8]
	Pickles	<i>Lc. mesenteroides</i> , <i>P. cerevisiae</i> , <i>Lb. brevis</i> , <i>Lb. plantarum</i>	
	Fermented olives	<i>Lb. paracasei</i> , <i>Lb. pentosus</i> , <i>Lb. plantarum</i>	
	Fermented vegetables	<i>P. acidilactici</i> , <i>P. pentosaceus</i> , <i>Lb. plantarum</i> , <i>Lb. fermentum</i>	
Meat Products	Vegetable juices	<i>Lb. acidophilus</i> , <i>Lb. bavaricus</i> , <i>Lb. bifidus</i> , <i>Lb. brevis</i> , <i>Lb. casei</i> , <i>Lb. delbrueckii</i> , <i>Lb. helveticus</i> , <i>Lb. plantarum</i> , <i>Lb. salivarius</i> , <i>Lb. xylosus</i> , <i>L. lactis</i> , <i>Lc. mesenteroides</i>	[3]
	Sausages	<i>P. acidilactici</i> , <i>P. pentosaceus</i> , <i>Lb. sakei</i> , <i>Lb. curvatus</i> , <i>Lb. plantarum</i> , <i>Lb. pentosus</i> , <i>Lb. casei</i> , <i>L. lactis</i>	[124,131]
Fermented Beverages	Wine	<i>Oenococcus oeni</i> , <i>Lb. plantarum</i> , <i>Lb. hilgardii</i>	[3]

Table 4. Criteria for the selection of starters for fruits and vegetables, cereal, dairy and meat fermentation.

Criteria Category	Fruits and Vegetables	Dairy Products	Meat Products	Cereal Based Foods
Technological	<ul style="list-style-type: none"> - Growth and acidification rate - Salt tolerance - Tolerance to low values of pH - Growth at low temperature - Completeness of fermentation - Malolatic fermentation - Tolerance to phenols - Synthesis of antimicrobial substances - No formation of hydrogen peroxide - Pectinolytic activity 	<ul style="list-style-type: none"> - Growth and acidification rate - Production of nutraceuticals - Accelerate ripening of cheese - Resistance to bacteriophage - Proteinase and peptidase activity 	<ul style="list-style-type: none"> - Fast production of lactic acid - Growth rate at different temperatures - Salt and pH tolerance - Persistence over the whole fermentation and ripening process - Nitrate and nitrite reduction - Catalase positive - Lactose negative - Proteolytic and lipolytic enzyme activities - No formation of hydrogen peroxide - Antagonism against pathogens - Improve the nutritional value of the sausages 	<ul style="list-style-type: none"> - Growth and acidification rate - Salt tolerance - Growth at low temperatures - Synthesis of antimicrobial compounds
Sensory	<ul style="list-style-type: none"> - Hetero-fermentative metabolism - Synthesis of aroma compounds and their precursors 	<ul style="list-style-type: none"> - Production of aroma and flavor - Synthesis of exopolysaccharides 	<ul style="list-style-type: none"> - Formation of flavor - Hetero-fermentative metabolism 	<ul style="list-style-type: none"> - Hetero-fermentative metabolism - Synthesis of aroma compounds and their precursors
Nutritional	<ul style="list-style-type: none"> - Synthesis of exopolysaccharides - Increase of the antioxidant activity - Synthesis of biogenic compounds - Bacteriocin production 	<ul style="list-style-type: none"> - Synthesis of exo-polysaccharides - Bacteriocins production - Reduction of toxic or antinutritional factors - Low-calorie sugar production - Vitamin production - Bioactive peptide production - Production of conjugated linolein acid (CLA) 	<ul style="list-style-type: none"> - Tolerance or even synergy to other microbial components or starters - No formation of ropy slime - Bacteriocin production - Probiotic features 	<ul style="list-style-type: none"> - Release of free amino acids - Synthesis of biogenic compounds - Degradation of antinutritional factor (phytic acid) - Increase the antioxidant activity - Synthesis of exopolysaccharides
Safety	<ul style="list-style-type: none"> - No formation of biogenic amines - No antibiotic resistance profile 			

The synthesis of exopolysaccharides (EPS) could be searched, especially for dairy and bakery products, for both sensory and nutritional reasons. According to their composition, EPSs are divided into homopolysaccharides (HoPS) and heteropolysaccharides (HePS). HePSs are composed of repeated units consisting of two or more monosaccharides, mainly galactose, glucose, fructose and rhamnose. HoPS are composed of repeated units of one monosaccharide, mainly glucose or fructose, and are classified in α -D-glucans (dextran, mutan, reuteran and alteran) or in β -D-glucans (levan and inulin-types). EPSs are produced intracellularly or extracellularly, and some bacteria are able to produce capsular EPS (CPS), which are covalently bound to the cell surface. In food industry, EPS are used as viscosifier, water-binding or gelling agents, stabilizers, texturizers and emulsifiers. Besides, EPS may act as antioxidant, antitumor, antiulcer and exert immune-modulating and cholesterol-lowering activities [132].

The ability to increase antioxidant activity is another criterion used to select functional starters for fruits and vegetables fermentation [7]. Several studies demonstrated that lactic acid fermentation increased the polyphenol content associated with an increase of the antioxidant activity [133–136]. This increase is mainly explained by enzymatic depolymerization of phenolic compounds by LAB [137], leading to more efficient uptake and higher bioavailability of plant polyphenols.

4.3. Non-Expected Characteristics of Starters

Despite of its antimicrobial activity, H_2O_2 is non-desired for some fermented products, especially in fermented sausages. Indeed, H_2O_2 can react and degrade organic and antioxidant compounds, increase rancidity and form a discoloration of the final product [7,124]. Papamanoli et al. [107] reported that 100% of *Lb. plantarum* strains (7), 58% of *Lb. curvatus* strains (24) and 84% of *Lb. sakei* strains (49) were able to produce H_2O_2 . It is surprising to note that these species are the main used as starters for fermented sausages.

Others LAB characteristics, which are non-desired for their use as starters, are those associated with health disorders. In particular, biogenic amines, which are organic bases mainly formed by the decarboxylation of amino acids, caused a number of outbreaks, resulting from fish or cheese consumption [138]. Histamine, putrescine, cadaverine, tyramine and β -phenylethylamine are the biogenic amines most frequently found in fermented foods like cheese, wine, sausages, beer, sauerkraut and fish. Bacteria associated with biogenic amines poisoning belong to the *Enterobacteriaceae* family, such as *Morganella morganii*, *Klebsiella pneumonia* and *Hafnia alvei*. Despite the fact that LAB could produce biogenic amines, no study has reported food poisoning resulting from LAB activities.

4.4. Improvement of Starters

Together with the starter research, several tools have been developed these last decades in order to enhance technological, sensory and nutritional properties of selected starters. Genetic and metabolic engineering facilitates the manufacturing of new starters expected to be superior to that found naturally [139]. It consists in adding or deleting some desired or non-desired criteria, altering a specific trait of a starter or transferring into another more preferable strain. Several tools have been used to develop new interesting and performant starters, such as the use of plasmid vectors, chromosome modification and expression systems, genetic mutants or engineering strains with genes from other LAB or other bacteria [140]. For instance, the gene encoding a bacteriocin from *Lb. helveticus* was introduced into *Lb. acidophilus* using a recombinant plasmid [141]. Genes encoding peptidases from a proteolytic *Lb. helveticus* strain were introduced into *L. lactis*. New peptidolytic activities were conferred to *L. lactis* with the aim to accelerate cheese ripening process [142]. Generally, independently of genetic methods used, starter genome sequencing is necessary and constitutes the model for starter engineering. However, authorization for producing these kind of microorganisms is necessary in most countries and consumers are reluctant regarding the use of genetically modified microorganisms in food industry.

Evolutionary engineering is currently the most promising direction for the improvement of starters. It consists of repeated steps of batch cultivation strains in the presence of a selective pressure or under selective conditions. The aim of serial batch cultivations is to increase genetic diversity resulting from mutations. Some mutants will survive and grow better under specific conditions than the initial strains [143,144]. Evolutionary engineering is largely investigated for *Saccharomyces cerevisiae* [145] and application on LAB deserves a deeper investigation. Experimental evolution has been performed on *L. lactis* KF147 strain, isolated from mung-bean sprouts [146]. The particularity of this strain is its poor growth in milk compared to other dairy *L. lactis* strains. *L. lactis* KF147 was serially cultivated for 1000 generations in skimmed milk and three mutants were selected NZ5521, NZ5522, and NZ5523. The acidification rates of NZ5521, NZ5522 and NZ5523 were increased compared to KF147.

5. Investigation into Using *Weissella* spp. as a Starter

5.1. Acidification and Growth Performance

Acidification and growth performance are important criteria for the selection of starters. *W. koreensis* HO20 (and *Lc. citreum* H012) reached to 6.5 to 9.5 log·cfu·g⁻¹ of dough and decreased the pH from 6.4 to 4.4 after 24 h of sourdough fermentation [147]. As a comparison, *Lb. plantarum* and *Leuconostoc* spp. reached to 6.5 to 9.5 log·cfu·g⁻¹ and 6.8 to 9.2 log·cfu·g⁻¹ of dough, respectively after 20 h of sourdough fermentation [148]. *W. cibaria* MG1 decreased the pH from 6.8 to 4.3 during the fermentation of different sourdough (buckwheat, quinoa, teff and wheat) [149]. *W. confusa* PE36, *Lb. plantarum* PE21 and *Lb. curvatus* PE4 grew from 4.5 to 8.9 log·cfu·g⁻¹ and decreased the pH from 5.0 to 3.7 after 15 h of fermentation of red and yellow peppers [150]. *W. thailandensis* was not able to acidify milk compared to *Lactobacillus* spp. [75]. Growth and acidification capacities of *Weissella* species in food fermentation, more precisely *W. cibaria*, *W. confusa* and *W. koreensis* are similar to those observed for *Lactobacillus* or *Leuconostoc*.

5.2. Production of Exopolysaccharides

Commercial production of EPS has focused mainly on dextran producing *Leuconostoc* species. However, several studies reported the production of EPS by *Weissella* spp. (Table 5). EPS are generally produced at levels of 10 mg·L⁻¹ to 1 g·L⁻¹ and have high molecular mass (10⁶ Da). Dextran from *Weissella* spp. harbor a molecular mass between 10⁴ and 10⁸ Da. Dextran of *Weissella* may be an alternative for the industry. Dextran production by *W. cibaria* MG1 during sourdough fermentation was reported by [149,151]. *W. cibaria* MG1 produced a significant higher amount of EPS (8 g/Kg) than *Lb. reuteri* Y2 and VIP (0.6 and 3.28 g/Kg, respectively) in sourdough. *W. cibaria* WC4 and *Lb. plantarum* PL9 produced the same amount of EPS during sourdough fermentation (2.5 g/Kg). Besides, these two strains increased the viscosity and the resulting bread showed a higher volume and a lower firmness [10]. Production of levan and CPS have been also described for some *W. confusa* strains [152]. Since *Weissella* spp. are able to grow in sourdough and produce a high amount of EPS, they present an interest as starters for industrial production of sourdough.

Table 5. Characterization of EPS from *Weissella* species.

Species	Source	Type of EPS	Molecular Mass (Da)	Amount Produced	Media	Reference
<i>W. cibaria</i> (WC4)	Sourdough	Glucan	1.1–1.3 × 10 ⁴	7.9 g·L ⁻¹ (6 d) 2.5 g·kg ⁻¹	MRS + Sucrose Sourdough	[10]
<i>W. cibaria</i> (WC3)	Sourdough	Glucan	1.1–1.3 × 10 ⁴	6.7 g·L ⁻¹ (6 d)	MRS + Sucrose	[10]
<i>W. cibaria</i> (WC9)	Sourdough	Glucan	1.1–1.3 × 10 ⁴	5.5 g·L ⁻¹ (6 d)	MRS + Sucrose	[10]

Table 5. Cont.

Species	Source	Type of EPS	Molecular Mass (Da)	Amount Produced	Media	Reference
<i>W. cibaria</i> (MG1)	Sourdough	Dextran	10^6 to 10^7	0.9 g·kg ⁻¹	Sourdough	[149]
				3.2 g·kg ⁻¹		
				4.2 g·kg ⁻¹		
				8 g·kg ⁻¹		
			7.2×10^8	36.4 g·L ⁻¹	MRS + Sucrose	[153]
<i>W. cibaria</i> (11GM-2)	Sour milk	Dextran	$>2 \times 10^7$	ND	MRS + Sucrose	[152]
<i>W. cibaria</i> (CMGDEX3)	Cabbage	Dextran	$>2 \times 10^6$	0.24 g·L ⁻¹	MRS + Sucrose	[154]
<i>W. cibaria</i> (JAG8)	Apple	Dextran	8×10^5	38 g·L ⁻¹ (12 h)	Tsuchiya medium	[155,156]
<i>W. confusa</i> (E392)	Soured carrot mash	Dextran	ND	ND	MRS + Sucrose	[157]
<i>W. confusa</i> (KR780676)	Idli batter	Galactan	ND	17.2 g·kg ⁻¹ (dry weight)	MRS + Sucrose	[87]
<i>W. confusa</i> (F3/2-2)	Cassava fermentation	Dextran	$>2 \times 10^7$	ND	MRS + Sucrose	[152]
		Levan	2×10^5	ND	MRS + Raffinose	
<i>W. confusa</i> (8CS-2)	Sour milk	HePS	ND	ND	MRS + Glucose	[152]
		Dextran	$>2 \times 10^7$	ND	MRS + Sucrose	
<i>W. confusa</i> (NH 02)	Nham	ND	1.13×10^6	18.08 g·L ⁻¹	MRS + Sucrose	[104]
<i>W. hellenica</i> (SKkimchi3)	Kimchi	Glucan	2.03×10^5	5.12 g·L ⁻¹	MRS + Sucrose	[45]

The effect of EPS-producing *Weissella* was also investigated on vegetable puree. Dextran from *W. confusa* and *Lc. lactis* was able to improve the texture and sensory properties of pureed carrots, with pleasant odor and flavor [158].

5.3. Production of Antimicrobial Substances

Ayeni et al. [68] determined lactic acid, acetaldehyde, acetone and ethanol amount production of *W. confusa*, *Lb. brevis* and *Lb. paracasei* strains after 24 h of culture in MRS broth. *W. confusa* strains produced 13.2 to 15.9 mg·mL⁻¹ lactic acid, 15.8 to 32.8 µg·mL⁻¹ acetone, 35.1 to 64.0 µg·mL⁻¹ acetaldehyde and 2.7 to 5.0 mg·mL⁻¹ ethanol while *Lactobacillus* strains produced 13.7 to 21.8 mg·mL⁻¹ lactic acid, 4.0 to 38.1 µg·mL⁻¹ acetone, 12.6 to 42.4 µg·mL⁻¹ acetaldehyde and 0.01 to 4.3 mg·mL⁻¹ ethanol in the same conditions. The lowest production of lactic acid was observed for *W. confusa*. However, the highest productions of acetaldehyde and ethanol were observed for *W. confusa* strains. *W. koreensis* HO20 has been shown to produce more ethanol than *Lc. citreum* HO12 during sourdough fermentation (4.7 and 3.0 mmol·kg⁻¹ dough) [147].

W. cibaria and *W. confusa* strains showed the same antimicrobial activity against *E. coli* K12 than *Lb. fermentum*, *Lb. plantarum* and *P. curvatus* strains, however this activity was strain dependent. *W. cibaria* strains showed zones of inhibition comprised between 14.5 and 23.5 mm, while those of *Lb. fermentum* strains were comprised between 16.2 to 23.2 mm. Anyway, the highest antagonist activity against *E. coli* was observed for *W. cibaria* 142 [60]. In addition, *W. confusa* has been shown to inhibit the growth of *Helicobacter pylori* [159].

Bacteriocins isolated from *Weissella* spp. have been extensively reviewed by [18]. Weissellicin 110, produced by *W. cibaria* 110 was active against several LAB, including *Lactobacillus*, *Leuconostoc* and *Weissella* species [117]. Several other bacteriocins have been purified from *W. hellenica* strains (weissellicins D, L, M, Y, 7293A and 7293B) and *W. paramesenteroides* (weissellicin A) [114,160–163]. Weissellicin L presented a high homology with leucocin B-TA33a, produced by *Lc. mesenteroides* TA33a. More recently, Weissellicin MBF has been characterized from *W. confusa* [164]. Interestingly, weissellicin MBF is encoded by a large transferable plasmid of 17.6 kbp, pWcMBF8-1. To the best of our knowledge, this is the first study which reported plasmid-associated bacteriocin activity in the genus *Weissella*.

5.4. Probiotic Aspects

Probiotics can be defined as living microorganisms which once ingested exert health beneficial properties. The criteria for the selection of probiotics are: (1) the ability to survive through the passage into the human gastrointestinal tract (GIT), that is to say low pH in the stomach and bile salts in the small intestine; (2) a human origin and isolation from healthy human GIT; (3) a non-pathogenic history; (4) not being associated with diseases; (5) not carrying transmissible antibiotic resistance genes and (6) the Generally Recognized as Safe (GRAS) status. Today, LAB associated with probiotic potential mainly belong to *Lactobacillus* and *Bifidobacterium* genera [165]. Recently, investigation of probiotic effect of *Weissella* spp. have gained [55,60,166].

Patel et al. [60] reported that *W. confusa* AI10 was the most resistant strain to bile salts (0.3%), with 72% of survival after 24 h at 37 °C. On the contrary, *Lb. plantarum* AD29 was the less resistant, with 14% of survival. In the same study, *W. cibaria* 142 showed 131% of survival after 2.5 h at 37 °C in MRS broth adjusted to pH 3, which demonstrated the ability of this strain to grow in acidic conditions. Reference [107] related that 100% of *Lb. plantarum* strains were resistant to 0.3% of bile salts and none of those strains were able to grow at pH 3. Anandharaj et al. [55] reported that *W. koreensis* FK121 was the best resistant strain to pH 1.0, with 29.8% of survival, while *Lb. crispatus* GI6 showed the lower resistance with 18.3% of survival. In this same study, *W. koreensis* and *Lb. crispatus* strains showed approximately the same resistance profile to 0.3% and 0.5% of bile salts. Hence, resistance to bile salts and to acidic conditions are strain dependent and regarding these criteria, probiotic activity should not be assigned to one specific LAB genus or species.

5.5. Role in Bioavailability and Antioxidant Activities

The increase of antioxidant activity occurring over lactic acid fermentation has been related to the activity of several enzymes, such as β -glucosidase (E.C. 3.2.1.21), tannase (E.C. 3.1.1.20), *p*-coumaric acid decarboxylase (PAD) (E.C. 4.1.1.102) or feruloyl esterase (E.C. 3.1.1.73). These enzymes have been largely described in *Lactobacillus* and *Bifidobacterium* spp. [167–171]. Concerning *Weissella* spp., only a few studies reported these activities.

β -glucosidases catalyze the hydrolysis of diverse compounds with β -D-glucosidic linkages, like oligosaccharides, cell wall components, pigments and cyanogenic glucosides [172]. β -glucosidases have been used in lactic acid fermentation to convert isoflavones glucosides into their corresponding aglycones [173]. Isoflavones constitute a subfamily of the flavonoids. It has been suggested that isoflavones aglycones are absorbed faster and in larger amounts than their corresponding glucosides in humans. Both tannase and β -glucosidase activities were reported for *Lb. plantarum*, *Lb. pentosus*, *Lc. mesenteroides* subsp. *mesenteroides* and *W. cibaria* strains, whereas only β -glucosidase activity was detected for *W. paramesenteroides* BFE 7601 [85]. *W. cibaria* and *W. confusa* strains showed up to 50-fold higher β -glucosidase activity than *L. lactis* subsp. *cremoris*. *W. confusa* has been shown to increase aglycone level in fermented soymilk as well as *Lb. paraplantarum* and *Streptococcus salivarius* [173]. Soymilk fermented for 12 h with *Weissella* spp. 4 (not identified) was 100-fold lower in isoflavones glucosides and 3-fold higher in aglycones than the one fermented with *Streptococcus infantarius* [174].

Phenolic acid decarboxylase is responsible for the decarboxylation of caffeic, *o*-coumaric and ferulic acids into their corresponding vinyl derivatives vinylcatechol, *o*-vinylphenol and vinylguaiacol, respectively. These vinyl derivatives can be reduced into ethylcatechol, ethylphenol and ethylguaiacol, respectively by the phenolic acid reductase. *W. cibaria/confusa* strains were shown to be able to reduce and decarboxylate caffeic, *o*-coumaric and ferulic acids. *Lb. brevis*, *Lb. fermentum*, *Lb. curvatus*, *Lc. mesenteroides* and *Lb. rossiae* were also able to metabolize these phenolic compounds [175]. Kimchi started with *W. koreensis* OK1-6 has been shown to decrease epididymal fat pad weight, leptin, triglyceride and cholesterol levels in obese mice [176], suggesting anti-obesity and anti-cholesterol effects of *W. koreensis* OK1-6.

6. Possible Constraints for the Use of *Weissella* spp. as Starters

6.1. Biogenic Amine Production of *Weissella*

Amino acids like histidine, lysine, ornithine and tyrosine can be decarboxylated by LAB in histamine, cadaverine, putrescine and tyramine, respectively. This ability is highly variable and often strain specific [177]. No production of biogenic amine from histidine, lysine, ornithine or tyrosine has been detected for *W. confusa* strains [118] neither by *W. cibaria* strains [178] nor by *W. viridescens* [110]. In these studies, the method used for the detection of biogenic amines was a qualitative method using bromocresol purple as a pH indicator. Using this method, *E. faecium* and *E. faecalis* were able to produce biogenic amines [110]. The detection of genes encoding amino acid decarboxylase would help to confirm these observations. On the contrary, some *Weissella* strains (*W. cibaria*, *W. confusa*, *W. paramesenteroides*) have been shown to produce higher amount of biogenic amines (cadaverine, putrescine, histamine and tyramine) than *Leuconostoc* strains [179]. *W. halotolerans* W22 and *Lb. hilgardii* X₁B were able to degrade arginine in putrescine using arginine deiminase or ornithine and arginine decarboxylation pathways [111,180]. Some strains of *Lb. brevis*, *Lb. hilgardii* and *P. pentosaceus* were able to produce tyramine and putrescine [181]. *W. hellenica* 15.32 has been shown to produce only histamine whereas *Lc. mesenteroides* and *Lb. sakei* strains produced histamine plus tyramine in the same conditions [182]. As for other LAB species, biogenic amine production was strain-dependent and some *Weissella* strains did not produce any of the biogenic amine searched.

6.2. Antibiotic Resistance Profile of *Weissella*

Antibiotics are frequently used by the health care industries to fight infections. The excessive and inappropriate use of antibiotics lead these last decades to a development of antibiotic resistance in bacteria. Nowadays, it is clearly established that LAB possess several antibiotic resistance genes, and the problem is that they can transfer these genes to pathogenic bacteria [183]. Hence, antibiotic resistance of LAB should be taken carefully regarding their use as starters or probiotics. Several studies reported antibiotic resistance profile of *Weissella* spp. *W. cibaria*, *W. confusa* and *W. paramesenteroides* strains have been shown to be resistant to streptomycin and gentamicin. Only *W. cibaria* strains were resistant to penicillin G [179]. Several strains of *Lb. fermentum*, *Lb. plantarum*, *W. cibaria*, *W. confusa* and *P. parvulus* were resistant to vancomycin, norfloxacin, gentamicin and kanamycin. The same strains were sensitive to erythromycin, chloramphenicol, ampicillin and tetracycline. Only a few strains of *W. cibaria*, *Lb. fermentum* and *Lb. plantarum* were resistant to polymyxin [60]. D'Aimmo et al. [184] analyzed antibiotic resistance profile of several strains of *Bifidobacterium animalis* subsp. *lactis*, *B. longum*, *Lb. acidophilus*, *Lb. casei* and *Lb. delbrueckii* subsp. *bulgaricus* and *S. thermophilus*. All tested strains were resistant to aztreonam, cycloserin, kanamycin, polymyxin B and spectinomycin. Several probiotics LAB have been associated with antibiotic resistance such as *Lb. reuteri* ATCC 55148, *Lb. brevis* ATCC 8287 and *Lb. plantarum* DG507 which have been shown to be resistant to vancomycin and erythromycin [185]. Since, *Lactobacillus* have been associated with fermented foods consumed for decades, they are considered as safe for humans. Hence, antibiotic resistance profile of these species is often neglected. From our point of view, *Weissella* genus should not be associated systematically with antibiotic resistance patterns on the grounds that some strains presented resistance to a low number of antibiotics. Besides, *Weissella* spp. share numerous habitats with *Lactobacillus*, *Leuconostoc*, *Lactococcus* and *Pediococcus*. All of these species have been associated with antibiotic resistance and each of them may transfer antibiotic resistance gene to each other. As evidence from literature data, antibiotic resistance is strain-dependent, and a careful analysis of each LAB strain should be realized before its application as starters for food fermentation.

6.3. Infections Associated with *Weissella*

Of the 21 *Weissella* species, only strains of *W. cibaria*, *W. confusa*, *W. paramesenteroides* and *W. viridescens* have been isolated from human clinical samples. *W. viridescens* and *W. cibaria* have

been associated with healthy human vaginal microbiota, together with *Lactobacillus*, *Leuconostoc*, *Pediococcus*, *Streptococcus* and *Enterococcus* [186–188]. Lee, (2005) [188] suggested *W. cibaria* PL9023 (*W. kimchi*) as a probiotic for women, since it has been shown to inhibit the growth of vaginal pathogens like *E. coli*, *Candida albicans* and *Streptococcus agalactiae*. *W. confusa*, *W. cibaria* and *W. paramesenteroides* have been isolated from healthy human feces [166,189–192]. Interestingly, *Weissella* spp. mainly isolated from healthy humans (*W. cibaria*, *W. confusa*, *W. paramesenteroides*, *W. viridescens*) are the same species frequently isolated from fermented foods. Since, they have been isolated from human vagina and feces, *Weissella* spp. may adhere and colonize the human GIT. These observations support data regarding resistance of *Weissella* to bile salts and acidic conditions.

Despite the fact that numerous *Weissella* spp. have been isolated from healthy humans and are suggested as probiotics, they are often classified as opportunistic pathogens since they were occasionally associated with infections. Actually, four *Weissella* species have been associated with health disorders and infections, both in animals or humans: *W. cibaria*, *W. confusa*, *W. viridescens* and *W. ceti*. *W. ceti* is considered to be a pathogen which infects fish and rainbow trout [193,194]. Genome sequence analysis of *W. ceti* strains revealed the presence of several virulence factors and antibiotic resistance genes [195], which comforts its potential pathogenicity. To the best of our knowledge, no study reported infections associated *W. ceti* in humans. *W. cibaria* and *W. viridescens* have been associated with bacteremia [18] and *W. cibaria* and *W. confusa* have been also isolated from dog ear otitis [37]. Concerning *W. confusa*, several cases reported bacteremia and infections [196–206]. In almost all cases of infections associated *W. confusa*, patients were immunocompromised or have undergone chemotherapy or organ transplant [207]. These organisms' weaknesses may facilitate the entry of *W. confusa* in the body. In almost all cases of *W. confusa* infections, vancomycin-resistance profile of these species has been point out.

In parallel, [208] reported more than 200 cases of related *Lactobacillus* associated infections. The *Lactobacillus* species most frequently associated with bacteremia are *Lb. casei* and *Lb. rhamnosus*. *Lactobacillus* spp. have been shown to be resistant to vancomycin and erythromycin in 27% and 97% of bacteremia associated *Lactobacillus*, respectively. Surprisingly, *Lactobacillus* are the main species used as starters or probiotics in food industries. Their potential pathogenicity does not deprive them of their safe status. Because immunodeficiency was the main risk factor of *Lactobacillus* bacteremia, [209] suggested that *Lactobacillus* bacteremia should be considered as a negative prognostic marker rather than a pathogen, suggesting comorbidities. Drawing a parallel between the two genera, *Weissella* spp. should not be considered as pathogens because *W. confusa* have been associated with bacteremia.

6.4. Bacteriophage Infection

Bacteriophages are ubiquitous, they are considered as the most predominant biological materials present in the world [210]. Phages infecting LAB have been associated with fermented products with inferior quality, especially in dairy products. Adsorption of phage particles to bacterial cells is the initial step of phage infection, then after phages inactivate and lyse microbial cells [211]. Only a few studies reported phages infecting *Weissella* spp. Bacteriophage Φ 22 from *W. cibaria* N22 was isolated from *Nham*, a Thai fermented pork sausage [212]. Both Φ 22 and Φ YS61 belong to the *Podoviridae* phage family and harbor size genome of 29 Kb and 33.6 Kb, respectively. Lu et al. [62] isolated 57 phages infecting *W. cibaria*, *W. paramesenteroides*, *Lb. plantarum* and *Lb. brevis* in commercial cucumber fermentation. Some phages were able to infect species from different genera, for instance Φ 3.2.27 was able to infect *W. cibaria*, *Lb. plantarum* and *Lb. brevis*. Interestingly, all *Weissella* hosts were isolated from day 3 of the fermentation process. The same authors isolated 28 bacteriophages infecting *Lc. citreum*, *Lc. mesenteroides*, *Lc. pseudomesenteroides*, *Lc. fallax*, *Weissella* spp., *Lb. plantarum*, *Lb. brevis* and *Lb. paraplantarum* in commercial sauerkraut [66]. Interestingly, all hosts isolated from days 1 and 3 of the fermentation process belong to *Leuconostoc* and *Weissella*, while all hosts isolated after 3 days of fermentation belong to *Lactobacillus*. These observations are correlated to the dominance of *Weissella* spp. in fermented foods, where they appeared generally at the beginning of the fermentation

together with *Leuconostoc* spp. The authors suggested that bacteriophages may play an important role in the LAB succession occurred in vegetables fermentations. Hence, bacteriophages of *Weissella* would require a deeper investigation. The disappearance of *Weissella* observed in vegetables fermentation may be the consequence of dying cells caused by phage infections. The majority of phages infecting *Leuconostoc* spp. were isolated from dairy products but vegetable fermentation constitutes another source of phages infecting *Leuconostoc*, *Weissella* and *Lactobacillus* spp. [211]. Among LAB, *L. lactis*, *S. thermophilus* and *Lactobacillus* are the main bacteriophages infecting hosts. Indeed, the genome sequence of 58 phages infecting *L. lactis* have been published [213]. Repeated use of the same starter culture in the same raw material has been suggested to be a risk of phage infection. Thus, development of new starter cultures would be useful both for consumers and food industries.

6.5. Regulations

A substance commonly used in food prior to 1958 is recognized as GRAS (Generally Recognized as Safe) by the Food and Drug Administration (FDA) and the list includes fermentative microorganisms. Since 2007, food microorganisms with a safety assessment are listed as QPS (Qualified Presumption of Safety) by the European Food Safety Authority (EFSA). Probiotics are alive microorganisms which, when ingested in adequate numbers exert a health benefit on the host. Species such as *Enterococcus faecium*, *Lb. plantarum*, *Lb. acidophilus* and *Lb. casei* subsp. *rhamnosus* possess the GRAS status [185]. *Lactobacillus*, *Bifidobacterium*, *S. thermophilus* and *E. faecium* are the probiotics mainly used in the food industry [214].

Bourdichon et al. [215] created a list called “Inventory of Microbial Food Cultures”. The microbial species with a documented presence in fermented foods were included in this list. On the contrary, the species considered as undesirable in food, that do not harbor interested metabolic activity and with a lack of data related interested criteria in food fermentation were excluded of the list. Interestingly, the authors included *Weissella* species in this list as microorganisms with beneficial use.

However, *Weissella* spp. are still not recognized as GRAS by the FDA neither as QPS by the EFSA, so not as a probiotic since GRAS status is required as criteria for probiotic status.

Weissella spp. are frequently associated with *Lactobacillus*, *Leuconotocs*, *Lactococcus* and *Pediococcus* in different habitats, and in food fermentation *Weissella* spp. participate to the process but *Lactobacillus* spp. remained generally the dominant species. Since, *Lactobacillus* are used for centuries in food fermentation, they possess the GRAS status. Industrial people easily prefer using recognized safe LAB rather than those which are not.

7. Concluding Remarks

Starter selection is a complex and long process which requires several steps: (1) isolation and in vitro selection; (2) validation on a lab-scale; (3) validation at factory-scale [216]. Bevilacqua et al. [216] developed a general flow-sheet for the selection of suitable yeast starter cultures, but it can easily be adapted for LAB (Figure 2). Starter cultures may consist of a single culture or a multiple culture containing a mixture of several strains. Self-propagation of the starter culture was initially the preferred method, but with this method several LAB characteristics were lost [8] and it was gradually replaced by ready-to-use frozen, freeze-dried or lyophilized highly concentrated cultures [3,139]. However, the manufacturing of frozen and freeze-dried cultures are long and expensive steps, limiting the production and the development of starter.

Weissella species harbor different sources of habitats, fermented foods, animal, environment and human sources. They share these habitats with LAB commonly used as starters or probiotics, like *Lactobacillus*, *Leuconostoc*, *Lactococcus* and *Pediococcus* species. *Weissella* spp. are extensively involved in spontaneous fermented foods, especially fruits and vegetables based products, in which they could dominate the process.

Nowadays, *Weissella* proposal as starter is still under investigation at the lab-scale, whereas the genus was described 24 years ago. *Weissella* do not possess the GRAS status so it probably limits

investigation for use as starter. From the literature, scientists are divided about using *Weissella* spp. as starters. *Weissella* are often classified as opportunistic pathogens, which seems to be a limit for food application. Some LAB species used as commercial starters have been associated with biogenic amine production, antibiotic resistance profile and infections. Surprisingly, these non-expected characteristics do not deprive them of their GRAS status and even less of their commercial starter status. Infections associated *Weissella* strains do not justify their rejection as commercial starters, especially since infections associated *Weissella* is strain-dependent. *Weissella* spp. can be used as commercial starter but safety aspects of the selected *Weissella* strain need to be investigated.

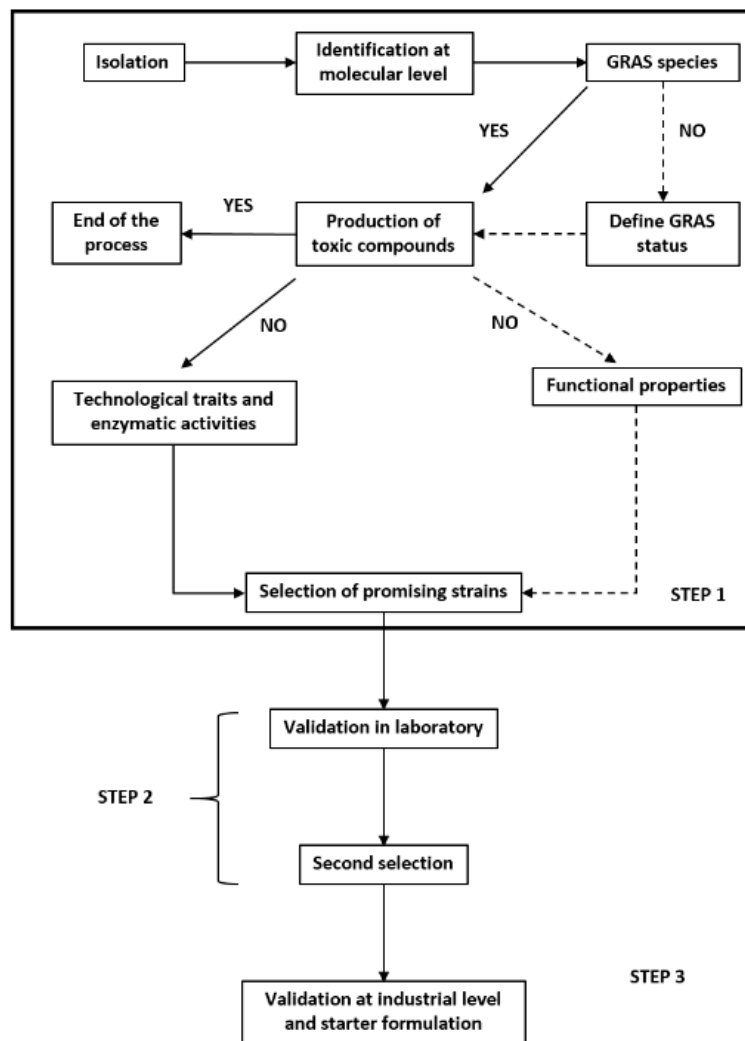


Figure 2. Flow-sheet for the selection of a starter [216]. Dotted line is for facultative paths.

Conflicts of Interest: The authors declare no conflict of interest.

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