The genus *Weissella*: taxonomy, ecology and biotechnological potential

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Bacteria assigned to the genus *Weissella* are Gram-positive, catalase-negative, non-endospore forming cells with coccoid or rod-shaped morphology (Collins et al., 1993; Björkroth et al., 2009, 2014) and belong to the group of bacteria generally known as lactic acid bacteria. Phylogenetically, the *Weissella* belong to the *Firmicutes*, class *Bacilli*, order *Lactobacillales* and family *Leuconostocaceae* (Collins et al., 1993). They are obligately heterofermentative, producing CO$_2$ from carbohydrate metabolism with either D(--), or a mixture of D(--)- and L(+) lactic acid and acetic acid as major end products from sugar metabolism. To date, there are 19 validly described *Weissella* species known.

*Weissella* spp. have been isolated from and occur in a wide range of habitats, e.g., on the skin and in the milk and feces of animals, from saliva, breast milk, feces and vagina of humans, from plants and vegetables, as well as from a variety of fermented foods such as European sourdoughs and Asian and African traditional fermented foods. Thus, apart from a perceived technical role of certain *Weissella* species involved in such traditional fermentations, specific *Weissella* strains are also receiving attention as potential probiotics, and strain development of particularly *W. cibaria* strains is receiving attention because of their high probiotic potential for controlling periodontal disease. Moreover, *W. confusa* and *W. cibaria* strains are known to produce copious amounts of novel, non-digestible oligosaccharides and extracellular polysaccharides, mainly dextran. These polymers are receiving increased attention for their potential application as prebiotics and for a wide range of industrial applications, predominantly for bakeries and for the production of cereal-based fermented functional beverages. On the detrimental side, strains of certain *Weissella* species, e.g., of *W. viridescens*, *W. cibaria* and *W. confusa*, are known as opportunistic pathogens involved in human infections while strains of *W. ceti* have been recently recognized as etiological agent of “weissellosis,” which is a disease affecting farmed rainbow trouts. Bacteria belonging to this species thus are important both from a technological, as well as from a medical point of view, and both aspects should be taken into account in any envisaged biotechnological applications.

Keywords: lactic acid bacteria, probiotic, prebiotic, bacteriocin, food safety, food quality, fermented food, detection and typing
A Brief Look at the History of Weissella Taxonomy

Collins and colleagues were the first to designate the genus Weissella in 1993 after taxonomic studies on atypical Leuconostoc-like microorganisms which stemmed from fermented sausages produced in Greece. Collins et al. (1993) noticed that these bacteria differed from other Leuconostoc species in a number of biochemical tests. Furthermore, molecular systematic investigations suggested that leuconostocs could be separated into three distinct genetic lineages, i.e., the genus Leuconostoc sensu stricto, the L. paramesenteroides group (which included also the atypical lactobacilli) and the species then known as L. oenos (which is currently classified as Oenococcus oeni). An in-depth study based on phenotypic, biochemical and 16S rRNA gene analyses allowed the differentiation of the new genus Weissella (gen. nov.) and the re-assignment of the species previously grouped in the genus Lactobacillus as W. confusa, W. halotolerans, W. kandleri, W. minor, and W. viridescens. In addition, one species previously assigned to the genus Leuconostoc, i.e., W. paramesenteroides, was also included in the new genus (Collins et al., 1993).

These species, as well as a newly described, coccus-shaped isolate W. hellenica reported in the study of Collins et al. (1993), all shared high 16S rRNA gene sequence similarity, warranting them to be included into the new genus Weissella. Unusual in this respect was that all Lactobacillus species at that time were considered to be of rod shape, while species of the genus Leuconostoc were often reported as cocci. Actually, the leuconostocs do not form perfectly round cells but are rather of lentil-like shape, i.e., with tapered ends, which Collins et al. (1993) referred to as “typical irregular coccoid morphology.” Nevertheless, the newly described genus Weissella comprises bacteria which are either cocci or rods in shape.

Bacteria belonging to the genus Weissella are difficult to separate from members of the genera Leuconostoc or the heterofermentative lactobacilli on the basis of phenotypic characteristics only. As mentioned above, the taxonomy of the closely related bacteria in these groups, and the new description of the genus Weissella, was possible only on the basis of molecular taxonomic techniques. The genus Weissella was named after the German microbiologist Norbert Weiss, known for his many contributions in the field of lactic acid bacteria research (Collins et al., 1993). Since the original description of the genus by Collins et al. (1993), various new species of Weissella have been described, so that currently the genus comprises 19 validated species (Figure 1). Key to these new species descriptions in the relevant studies were 16S rRNA gene sequence and DNA:DNA hybridization analyses, together with phenotypic data in a polyphasic taxonomic approach. Thus, the Weissella species grouped in five phylogenetic branches based on 16S phylogeny, with W. soli, W. dies-trammenae, W. koreensis, W. kandleri, and W. oryzae as members of the first branch, W. cibaria and W. confusa as members of a second and W. thailandensis, W. helenica and W. paramesenteroides occurring in a third branch. W. ceti, W. halotolerans, W. viridescens, W. minor, and W. uvarum are associated with the fourth branch, and W. beninensis, W. fabalis, W. fabaria, and W. ghanensis with the fifth (Figure 1). De Bruyne et al. (2010) showed that an improved phylogeny of Weissella based on pheS gene sequences was possible, due to the higher discriminatory power of this marker gene when compared to the 16S rRNA gene. Based on the pheS phylogenetic investigation (Figure 1), the authors showed that the new species described in that study as W. fabaria, together with the already described W. ghanensis species clustered together as a first divergent line within the genus Weissella. Subsequent to the study of De Bruyne et al. (2010), two further novel species, i.e., W. beninensis and W. fabalis were described (Padonou et al., 2010; Snaauwaert et al., 2013) that also grouped together with W. fabaria and W. ghanensis into a well-defined cluster. Thus, these four species appear to constitute this first divergent line of species within the genus Weissella. The term “species groups” has been previously used to group species that occur in phylogenetically closely related groups as in the case, e.g., for the enterococci (Svec and Franz, 2014). This has so far not been done for species occurring in the genus Weissella. Based on the clear grouping of species into 5 well-defined clusters, these groups could be designated as the W. kandleri, W. confusa, W. halotolerans, W. paramesenteroides, and W. beninensis species groups, respectively.

General Description of Bacteria Belonging to the Genus Weissella

Bacteria belonging to the genus Weissella are Gram-positive, catalase-negative, non-endospore forming cells with coccoid or rod-shaped morphology (Collins et al., 1993; Björkroth et al., 2009, 2014). The Weissella species belong to the phylum Firmicutes, class Bacilli, order Lactobacillales and family Leuconostocaceae (Collins et al., 1993). Only W. beninensis was reported to be motile (Padonou et al., 2010), with all other species being non-motile. As in the original description of the genus Weissella (Collins et al., 1993), the bacteria of this genus were described to be non-motile. As mentioned above, the motile characteristic of W. beninensis is not in accordance with the description of general characteristics of bacteria in this genus, and consequently the genus description was emended by Padonou et al. (2010) to account for atypical motility of this particular species. Weissella bacteria are facultatively anaerobic chemoorganotrophs with an obligatorily fermentative metabolism. They do not possess cytochromes and ferment glucose heterofermentatively via the hexose-monophosphosphate and phosphoketolase pathways. End products of glucose heterofermentation include lactic acid (with some species producing only D(−)-and others both D(−) −and L(+)-lactic acid enantiomers), gas (CO₂) and ethanol and/or acetate (Collins et al., 1993; Björkroth et al., 2014). The bacteria have complex nutritional requirements and need peptides, amino acids, fermentable carbohydrates, nucleic acids, fatty acids and vitamins for growth. All species grow at 15°C and some can grow up to 42–45°C. Production of dextran, hydrolysis of esculin and production of ammonia from arginine are variable characteristics for the different species, and may be used as phenotypic tests to aid in species identification (Table 1). The same applies for fermentation of sugars such as cellobiose, fructose, galactose, lactose, maltose, melibiose, raffinose, ribose, sucrose, trehalose and xylene (Table 1). The cell wall
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FIGURE 1 | Neighbor-joining phylogenetic tree based on (A) 16S rRNA sequences and (B) pheS gene sequences of Weissella species type strains. The 16S rRNA sequence of Bifidobacterium bifidum was used as an outgroup sequence. Bootstrap values (%) derived from 1000 replicates are given at branch points. Bar indicates % sequence divergence.

TABLE 1 | Differential characteristics of Weissella species.

| Characteristic          | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
|-------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| **ACID PRODUCED FROM**  |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| Arabinose               | −  | −  | +  | −  | −  | −  | −  | −  | −  | +  | −  | +  | −  | +  | +  | +  | +  | +  | +  | +  |
| Cellobiose              | d  | −  | +  | +  | ND | +  | +  | −  | −  | −  | −  | −  | +  | +  | +  | +  | +  | +  | +  | +  |
| Fructose                | +  | −  | +  | −  | +  | +  | +  | +  | +  | −  | −  | +  | ND | +  | +  | +  | +  | +  | +  | +  |
| Galactose               | +  | +  | −  | +  | −  | −  | −  | −  | −  | +  | −  | +  | −  | +  | +  | +  | +  | +  | +  | +  |
| Maltose                 | +  | +  | +  | +  | −  | −  | +  | −  | +  | +  | +  | +  | −  | +  | +  | +  | +  | +  | +  | +  |
| Melibiose               | +  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  |
| Raffinose               | d  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  | −  |
| Ribose                  | d  | +  | −  | +  | −  | −  | −  | −  | −  | +  | +  | +  | +  | +  | +  | +  | +  | +  | +  | +  |
| Succrose                | +  | −  | +  | +  | ND | −  | −  | d  | +  | −  | +  | −  | +  | +  | +  | +  | +  | +  | +  | +  |
| Trehalose               | d  | −  | −  | −  | +  | +  | −  | −  | +  | +  | +  | +  | d  | +  | +  | +  | +  | +  | +  | +  |
| Xylose                  | −  | −  | +  | +  | −  | −  | −  | −  | −  | +  | −  | −  | +  | +  | +  | +  | +  | +  | +  | +  |
| Esculin hydrolysis      | +  | +  | +  | +  | +  | −  | −  | −  | −  | +  | +  | +  | d  | −  | −  | +  | +  | +  | +  | +  |
| Ammonia from arginine   | +  | V  | +  | +  | +  | +  | +  | +  | +  | +  | +  | +  | +  | +  | +  | +  | +  | +  | +  |
| Dextran formation       | ND | +  | +  | +  | ND | +  | +  | +  | ND | +  | +  | +  | ND | +  | +  | +  | +  | +  | +  | +  |
| Lactic acid configuration| D  | D  | D  | D  | D  | D  | D  | D  | D  | D  | D  | D  | D  | D  | D  | D  | D  | D  | D  | D  |
| Mol% G+C content        | 37 | 39.2| 44–45| 45–47 | 45 | 37 | 38 | 40 | 44 | 39–40 | 39 | 37 | 44 | 40.6| 37–38 | 43 | 38–41 | 39.1| 41–44 |

Weissella species indicated as follows: 1, W. beninensis; 2, W. celti; 3, W. cibaria; 4, W. confusa; 5, W. diestrammenae; 6, W. fabalis; 7, W. fabaria; 8, W. ghanensis; 9, W. halotolerans; 10, W. hellenica; 11, W. kandleri; 12, W. koreensis; 13, W. minor; 14, W. oryzae; 15, W. paramesenteroides; 16, W. soli; 17, W. thailandensis; 18, W. viridescens. +, 90% or more strains are positive; -, 90% or more strains negative; d, 11–89% of strains positive; ND, no data available; v, variable.

Data partially adapted from Collins et al. (1993); Tanasupawat et al. (2000); Björkroth et al. (2002); Magnusson et al. (2002); De Bruyne et al. (2008, 2010); Vela et al. (2011); Oh et al. (2013); Snauwaert et al. (2013); Tohno et al. (2013) and Nisiotou et al. (2014).

Ecology

Bacteria of the genus Weissella inhabit a variety of ecological niches, including soil (mainly W. soli) (Magnusson et al., 2002; Chen et al., 2005), sludge of milking machines (W. minor) (Kandler et al., 1983), sediments of a coastal marsh (W. cibaria and W. confusa) (Zamudio-Mayá et al., 2008), sediments and fish from the Bahía Blanca estuary (W. viridescens) (Sica et al.,...
2010) and lake water (W. cibaria) (Yanagida et al., 2007), plants (Table 2), a huge variety of fermented foods (Table 3), the oral cavity, breast milk, the uro-genital and gastro-intestinal tracts of humans (Table 4), as well as the skin, milk and gastro-intestinal tract of many animals (Table 5).

Typical for lactic acid bacteria, to which the Weissella spp. belong, is their association with and adaptation to nutrient rich habitats (Makarova et al., 2006) including various food sources. Some Weissella species, i.e., W. viridescens, W. halotolerans, and W. hellenica, are mainly associated with meat and meat products, and were reported as part of the predominant microbiota responsible for quality fluctuations of packaged and chill-stored food products (Pothakos et al., 2014). Similarly, W. halotolerans has been reported to predominate in the microbial spoilage population of vacuum-packaged, charcoal-broiled European river lamprey (Lampetra fluviatilis) (Merivirta et al., 2005). W. viridescens causes spoilage of cured meats due to a green discoloration (Niven and Evans, 1957) and is involved in spoilage of the Spanish blood sausage Morcilla de Burgos (Santos et al., 2005; Koort et al., 2006; Diez et al., 2009) and of vacuum-packaged cooked sausages (Korkeala and Björkroth, 1997; Iacumin et al., 2014).

Weissella species are also commonly found in habitats associated with the human or animal body, e.g., the gastrointestinal tract or in human breast milk. W. cibaria was found to be present in all fecal samples from healthy adults, but less frequent in the fecal samples of celiac disease patients (Nistal et al., 2012). W. confusa was shown to be more widely distributed in the feces of non-irritable bowel syndrome patients than in the feces of patients affected by this disease (Ponnusamy et al., 2011). High loads of Weissella spp. were also found in the ileal microbiota of piglets fed with different amounts of zinc oxide (ZnO), an amphoteric molecule that is widely used as feed additive for the prophylaxis of diarrhea in piglets (Vahjen et al., 2010). W. confusa was found in the breast milk, as well as in the feces of both mothers and infants (Martín et al., 2007a; Albesharat et al., 2010), confirming the hypothesized mechanism of vertical transfer from the mother’s gut to the corresponding milk and subsequently from the milk to the infant’s gut. Regarding the presence of Weissella and other microorganisms in human milk, possible mechanisms by which these bacteria can reach the mammary gland (i.e., either by contamination or by active migration) have been reviewed recently (Jeurink et al., 2013). It has been suggested (Lahtinen et al., 2012) that Weissella strains from human milk, stem from an environmental source (e.g., soil, vegetation). Indeed, the mode of delivery at birth, the kind of diet, as well as the health status of humans and animals may affect the composition of the microflora of the oral cavity, the gastro-intestinal and uro-genital tracts. In agreement with this, by using a high-throughput sequencing approach, Belda et al. (2011) could show that W. paramesenteroides occurs at notably higher levels in the midgut of lab-reared populations of the European Corn Borer Ostrinia nubilalis than in the field population, in which gram-negative species were found to predominate. This probably was

### Table 2 | Occurrence of Weissella species in different environmental habitats.

| Species        | Habitat or Source                                                                 | References                           |
|----------------|-----------------------------------------------------------------------------------|--------------------------------------|
| W. cibaria     | Japanese horseradish, orange, pineapple, banana, chili bo                           | Endo et al., 2009                     |
|                | Tomatoes                                                                          | Di Cagno et al., 2009a               |
|                | Fluted pumpkin vegetable (Telfaria occidentalis) and green vegetable (Amaranthus spinosus) | Emererini et al., 2014               |
|                | Bee pollen                                                                        | Belhadi et al., 2014                 |
|                | Wheat flour                                                                       | Alfonzo et al., 2013                 |
|                | Corn stovers                                                                      | Pang et al., 2011                    |
|                | Blackberries                                                                      | Di Cagno et al., 2011                |
|                | Papaya                                                                            | Di Cagno et al., 2011                |
| W. confusa     | Rhizosphere of olive trees, soil surrounding rhizosphere                           | Fhoula et al., 2013                  |
|                | Raw red and yellow pepper                                                        | Di Cagno et al., 2009b               |
|                | Heroin                                                                            | Cho et al., 2014                     |
|                | Sugar cane and carrot juice                                                        | Hammes and Vogel, 1995               |
| W. halotolerans| Rhizosphere of olive tree, soil surrounding rhizosphere                            | Fhoula et al., 2013                  |
| W. hellenica   | Vegetative forage crops (mixed pasture of timothy and orchardgrass)              | Tohno et al., 2012                   |
| W. kandleri    | Heroin                                                                            | Cho et al., 2014                     |
| W. kincerely (W. cibaria) | Fluted pumpkin vegetable (Telfaria occidentalis) and green vegetable (Amaranthus spinosus) | Holzapfel and van Wyk, 1982          |
| W. paramesenteroides | Rhizosphere of olive trees                                                        | Emererini et al., 2014               |
|                | Fluted pumpkin vegetable (Telfaria occidentalis) and green vegetable (Amaranthus spinosus) | Fhoula et al., 2013                  |
|                | Chardonnay grapes, Semillon and Sauvignon Blanc grapes                            | Emererini et al., 2014               |
|                | Indian goosegrass                                                                 | Bae et al., 2006                     |
|                | Vegetative forage crops (mixed pasture of timothy and orchardgrass)              | Pang et al., 2012                    |
| W. soil        | Carrots                                                                           | Tohno et al., 2012                   |
|                |                                                                                   | Di Cagno et al., 2008                |
### TABLE 3 | Isolation of *Weissella* species from (fermented) foods.

| Species | Food source | Detection method | Country | References |
|---------|-------------|------------------|---------|------------|
| *Weissella* spp. | Joetgal (fermented sea food) | Pyrosequencing (culture-independent) | Korea | Roh et al., 2010 |
| *Weissella* spp., *W. paramesenteroides* | Mexican pozol (fermented maize dough) | Culture-independent PCR-DGGE | Mexico | Ampe et al., 1999 |
| *W. cibaria, W. soli, W. koreensis* | Dongchimi, (watery kimchi) | Pyrosequencing (culture-independent) | Korea | Jeong et al., 2013 |
| *Weissella* spp. *W. soli, W. beninensis* | Malt (produced by industrial malting) | Culture-independent T-RFLP (terminal restriction fragment length polymorphism) and pyrosequencing | Belgium | Justé et al., 2014 |
| *W. confusa, W. oryzae* | Unpasteurized Boza (cereal-based fermented beverage) | Culture-dependent 16S rRNA gene sequencing and culture-independent PCR-DGGE | Bulgaria | Osimani et al., 2015 |
| *W. hellenica, W. paramesenteroides* | Raw milk cheeses | Pyrosequencing of DNA and cDNA | Denmark | Masoud et al., 2012 |
| *W. confusa, W. cibaria* | Sourdough | Physiological and biochemical tests | France | Bounaix et al., 2010 |
| *W. cibaria, W. soli, W. minor, W. vinidescens* | Sorghum silage | Lab-made biochemical tests | Algeria | Chahrou et al., 2013 |
| *W. confusa* | Wheat sourdough | Culture dependent 16S rRNA sequencing | Italy | Corsetti et al., 2001 |
| | Cheese, Nono | Culture dependent partial 16S rRNA gene sequencing | Nigeria | Ayeni et al., 2011 |
| | Masai fermented milk | Physiological and biochemical tests | Northern Tanzania | Isono et al., 1994 |
| | Chili bo (Malaysian food ingredient) | Culture dependent: biochemical tests and 16S rRNA sequencing | Malaysia | Leisner et al., 1999 |
| | Suusac (fermented camel milk) | Culture-dependent 16S rRNA gene sequencing | Africa | Jansa et al., 2012 |
| | Emmer and spelt flour for bread making | Culture-dependent partial sequencing of recA, 16S/23S rRNA spacer region and pheS genes. | Italy | Coda et al., 2010, 2014 |
| | Cauliflower and mixed-vegetable spontaneous fermentation | Culture-dependent (GTG)5-PCR fingerprinting, 16S rRNA gene sequencing and culture-independent PCR-DGGE | Romania | Wouters et al., 2013 |
| | Togwa (Tanzanian fermented food) | Physiological and biochemical tests | Tanzania | Mugula et al., 2003 |
| | Douchi (salt-fermented soybean food) | Culture-dependent partial 16S rRNA sequencing | China | Liu et al., 2012 |
| | Bushera (fermented beverage) | Physiological and biochemical tests | Uganda | Muyanja et al., 2003 |
| | Stinky tofu (fermented tofu) | Culture-dependent 16S rRNA gene sequencing | Taiwan | Chao et al., 2008 |
| | Kulenaato (fermented milk) | Physiological and biochemical tests | Kenya | Mathara et al., 2014 |
| | Doenjang (fermented soybean paste) | Culture-independent PCR-DGGE | Korea | Kim et al., 2009 |
| | NtobaMbodi (fermented cassava leaves) | Culture-dependent partial 16S rRNA gene sequencing | Congo | Ouoba et al., 2010 |
| | Wheat sourdough | Culture-dependent partial 16S rRNA gene sequencing | France | Robert et al., 2009 |
| | Zichi (Sardinian sourdoughbread) | Culture-dependent 16S rRNA gene sequencing | Italy | Catzeddu et al., 2006 |
| | Kimchi | Culture-independent PCR-DGGE | Korea | Lee et al., 2005 |
| | Wheat sourdough | Culture-dependent partial 16S rRNA gene sequencing | France | Robert et al., 2009 |
| *W. cibaria* | Greek Traditional Wheat Sourdoughs | Culture-dependent DNA-DNA hybridization, and 16S ribosomal DNA sequence analysis | Greece | De Vuyst et al., 2002 |
| | Buckwheat and teff sourdoughs (spontaneously fermented) | Culture-dependent 16S rRNA gene sequencing and Culture-independent PCR-DGGE | Ireland | Moroni et al., 2011 |
| | Traditional Belgian sourdoughs | Culture-dependent 16S rRNA gene sequencing, DNA-DNA hybridization, REP-PCR and phenylalanyl-rRNA synthase (pheS) gene sequencing analysis | Belgium | Scheirlinck et al., 2007 |

(Continued)
| Species                        | Food source                                 | Detection method                                      | Country          | References                        |
|--------------------------------|---------------------------------------------|-------------------------------------------------------|------------------|-----------------------------------|
|                               | Nukadoko (naturally fermented rice bran mash used for pickling vegetables) | Pyrosequencing (culture-independent)                  | Japan            | Ono et al., 2014                  |
|                               | Buchwheat and teff sourdoughs               | Culture-dependent partial 16S rRNA sequencing          | Ireland          | Moroni et al., 2011               |
|                               | Fermented Jalapeño pepper                  | Culture-dependent partial 16S rRNA sequencing          | Mexico           | González-Quijano et al., 2014     |
|                               | Douchi (salt-fermented soybean food)       | Culture-dependent partial 16S rRNA sequencing          | China            | Liu et al., 2012                  |
|                               | Cassava                                     | Physiological and biochemical tests; culture-dependent partial 16S rRNA sequencing | South Africa, Benin, Kenya, Germany | Kostinek et al., 2007            |
|                               | Plaa-som (Thai fermented fish product)      | Biochemical tests; culture-dependent partial 16S rRNA sequencing | Thailand         | Sirionnual et al., 2007           |
|                               | Yan-dong-gua (fermented waxgourd)           | Physiological analysis; culture-dependent RFLP and partial 16S rRNA sequencing | Taiwan           | Lan et al., 2009                  |
|                               | Stinky tofu                                 | Culture-dependent 16S rRNA gene sequencing             | Taiwan           | Chao et al., 2008                 |
|                               | Pickles                                     |                                                       | China            | Zhao et al., 2008                 |
|                               | Fu-tsai (fermented mustard)                 | Physiological analysis; culture-dependent RFLP and partial 16S rRNA sequencing | Taiwan           | Chao et al., 2009                 |
|                               | Yan-jiang (fermented ginger)                | Culture-dependent 16S rRNA gene sequencing             | Taiwan           | Chang et al., 2011                |
|                               | Tarhana (yogurt and wheat flour-based fermented food) | Culture-dependent sequencing of the 16S rRNA | Turkey           | Sengun et al., 2009               |
|                               | Thai fermented pork sausage                 | Culture-dependent biochemical tests and partial 16S rRNA gene sequencing | Japan            | Thongpasit et al., 2009           |
|                               | Jiang-gua (fermented cucumbers)             | Culture-dependent RFLP partial sequencing of the 16S rRNA | Taiwan           | Chen et al., 2012                 |
|                               | Plaa-som (fermented fish)                   | Culture-dependent ARDRA and partial sequencing of the 16S rRNA | Thailand         | Kopermsuba and Yunchalaid, 2010   |
|                               | W. ghanensis                                | Ghanaian cocoa beans fermentation                      | Ghana            | De Bruyne et al., 2008            |
|                               | W. kandleri                                 | Koumiss                                               | Mongolia         | Wu et al., 2009                   |
|                               | W. kimchi (re-classified as W. cibaria by Ennahar and Cai, 2004) | Culture-dependent 16S rRNA gene sequencing             | Korea            | Choi et al., 2002                 |
|                               | Kimchi (fermented cabbage)                 | Culture-dependent 16S rRNA gene sequencing             | Korea            |                                   |
|                               | Cauliflower and mixed-vegetable spontaneous fermentation | Culture-dependent (GTG)_5-PCR fingerprinting, 16S rRNA gene sequencing | Romania          | Wouters et al., 2013              |
|                               | Kimchi                                      | Culture-dependent morphological, physiological and chemotaxonomic tests, 16S rRNA gene sequencing | Korea            | Lee et al., 2002                  |
|                               | Kimchi                                      | Culture-independent 16S rRNA gene clone libraries     | Korea            | Park et al., 2010                 |
|                               | Kimchi                                      | Culture-dependent physiological tests, partial 16S rRNA gene sequencing and restriction enzyme analysis | Korea            | Cho et al., 2006                  |
|                               | W. halotolerans                             | Fermented sausage                                      | Portugal          | Pereira et al., 2009              |
|                               | Naturally fermented sausage                 | Physiological and biochemical tests                    | Greece           | Samelis et al., 1994              |
|                               | Jiang-gua (fermented cucumbers)             | Culture-dependent RFLP partial sequencing of the 16S rRNA | Taiwan           | Chen et al., 2012                 |
|                               | Croatian raw ewe’s milk cheeses             | Pyrosequencing (culture-independent)                  | Croatia          | Fuka et al., 2013                 |
|                               | Fermented sausage                           | Culture-dependent PCR-DGGE and 16S rRNA gene sequencing | Italy            | Urs et al., 2006                  |
|                               | Sausage                                     | Culture-dependent PCR-DGGE and partial 16S rRNA gene sequencing | Italy            | Cocolin et al., 2009              |

(Continued)
TABLE 3 | Continued

| Species            | Food source                                      | Detection method                                                                 | Country      | References                  |
|--------------------|--------------------------------------------------|------------------------------------------------------------------------------------|--------------|-----------------------------|
| *W. minor*         | Gari (fermented cassava)                         | Physiological and biochemical tests; culture-dependent partial 16S rRNA sequencing | Africa       | Kostinek et al., 2005       |
|                    | Sludge of milking machines                       | 16S rRNA gene sequencing, DNA-DNA hybridization                                   | Germany      | Kandler et al., 1983        |
| *W. paramesenteroides* | Fermented sausage                                | Culture-dependent PCR-DGGE and 16S rRNA gene sequencing                            | Italy        | Urso et al., 2006           |
|                    | Goat's milk cheese                               | API 50 CH and API 20 STREP systems (Biomerieux)                                   | Spain        | Mas et al., 2002            |
|                    | Joetgal (fermented sea food)                     | Culture-independent PCR-DGGE                                                      | Korea        | Roh et al., 2010            |
|                    | Nukadoko (naturally fermented rice bran mash used for pickling vegetables) | Pyrosequencing (culture-independent)                                             | Japan        | Ono et al., 2014            |
|                    | Douchi (salt-fermented soybean food)             | Culture-dependent partial 16S rRNA sequencing                                       | China        | Liu et al., 2012            |
|                    | Croatian raw ewe’s milk cheeses                  | Pyrosequencing (culture-independent)                                              | Croatia      | Fuka et al., 2013           |
|                    | Yan-dong-gua (fermented waxgourd)                | Culture-dependent PCR-DGGE and 16S rRNA gene sequencing                            | Taiwan       | Lan et al., 2009            |
|                    | Stinky tofu                                      | Culture-dependent PCR-DGGE and partial 16S rRNA gene sequencing                   | Taiwan       | Chao et al., 2008           |
|                    | Fu-tsai                                          | Culture-dependent partial sequencing of the 16S rRNA, rpoA, pheS and dnaA genes    | Taiwan       | Chao et al., 2009           |
|                    | Cassava                                          | Culture-dependent physiological and biochemical tests, partial 16S rRNA gene sequencing | South Africa, Benin, Kenya, Germany |                 |
| *W. sol*           | Stinky tofu                                      | Culture-dependent phenotypic and chemotaxonomic tests, partial 16S rRNA gene sequencing | Taiwan       | Chao et al., 2008           |
| *W. taj-apia*      | Honey                                            | 16S rRNA gene sequencing                                                          | Malaysia     | Tajabadi et al., 2012       |
| *W. thailandensis* | Pla-ra and pla-chom (fermented fish)             | Phenotypic and chemotaxonomic tests; culture-dependent partial 16S                | Thailand     | Tanasupawat et al., 1998, 2000 |
| *W. viridescens*   | Dry-fermented sausage                            | Culture-dependent [GTG]5-PCR fingerprinting, 16S rRNA gene sequencing             | Greece       | Papamanoli et al., 2003     |
|                    | Cauliflower and mixed-vegetable spontaneous fermentation |                                                                                   | Romania      | Wouters et al., 2013         |
|                    | Nham (Thai-fermented pork sausage)               | Culture-dependent physiological and biochemical tests, 16S rRNA gene sequencing   | Thailand     | Pringsulaka et al., 2011    |
|                    | Doenjang (fermented soy bean paste)              | Culture-independent PCR-DGGE                                                      | Korea        | Kim et al., 2009            |
| *W. uvarum*        | Wine grapes                                      | 16S rRNA gene sequencing, DNA-DNA hybridization                                   | Greece       | Nisiotou et al., 2014       |

*Weissella taj-apia* described by Tajabadi et al. (2012) is currently an unvalidated species description.

the result of an increase in cell numbers due to the multiplication of these bacteria in the artificial diet prior to insect feeding. This finding led to the hypothesis that food exerts a selection pressure on the intestinal microbiota (Belda et al., 2011).

**Weissella Strains Associated with Human Clinical Infections**

*Weissella* strains have been isolated from clinical specimens such as blood, skin, infected wounds and feces of both humans and animals (Table 6). Apart from Kulwichit et al. (2007), who identified a *Weissella* strain from the blood of a patient as *W. viridescens*, and others from urine, lung swabs and blood of patients with bacteremia as *W. cibaria*, the only species of *Weissella*, which have been described as opportunistic pathogens of humans or as emerging pathogen for farmed rainbow trouts are *W. confusa* and *W. ceti*, respectively. In particular, *W. confusa* was isolated from several human and clinical specimens in cases of polymicrobial infections (Green et al., 1990, 1991; Riebel and Washington, 1990; Bantar et al., 1991; Olano et al., 2001; Björkroth et al., 2002). The isolation of the strains from polymicrobial infections did not allow an unequivocal clinical significance of this species. Subsequently, however, this species was also described as sole microbial agent in various infections which allowed the description of *W. confusa* as an opportunistic pathogen. Indeed, *W. confusa* was the causative agent of infections such as a systemic infection in a mona monkey (*Cercopithecus mona*) (Vela et al., 2003), a fatal case of endocarditis (Flaherty et al., 2003), a severe infective endocarditis of native valves (Shin et al., 2007), a postoperative osteomyelitis with chronic discharge in a young female (Kulwichit et al., 2007).
TABLE 4 | Weissella species in saliva, feces and vagina of humans.

| Species | Habitat or Source | References |
|---------|------------------|------------|
| W. cibaria | Children’s saliva (4–7 years old) | Kang et al., 2006a,b |
| Human saliva | | Kang et al., 2011 |
| Human feces | | Wang et al., 2008 |
| Human vagina | | Nistal et al., 2012 |
| | | Nam et al., 2007 |
| W. confusa | Human faeces | Ponnumary et al., 2011 |
| Human faeces (adults, mothers and babies) | | Albeshar et al., 2011 |
| Human faeces | | Zhang et al., 2014 |
| | | Walter et al., 2001 |
| W. confusa and W. Cibaria | Human faeces | Gomathi et al., 2014 |
| | Breast milk, vaginal swab and infant faeces | Martin et al., 2007a,b |
| W. kimchii (W. cibaria) | Human vagina | Lee, 2005 |
| Human vagina | | Jin et al., 2007 |
| W. parame- 
stenoides | Feces of breast-fed infants | Rubio et al., 2014 |
| W. vinides- 
scens | Human vagina | Silvester and Dicks, 2003 |
| | | Jin et al., 2007 |

TABLE 5 | Weissella species in healthy animals’ milk and skin.

| Species | Habitat or Source | References |
|---------|------------------|------------|
| Weissella spp. | Ileal digesta of piglets fed diets supplemented with 200 or 3000 ppm ZnO | Vahjen et al., 2010 |
| W. cibaria | Camel’s milk | Merzouk et al., 2013 |
| Goat’s milk | Elavarasi et al., 2014 |
| Feces of individually (healthy) owned dogs | Graef et al., 2005 |
| Acquatic animals | Muñoz-Atienza et al., 2013 |
| Feces of farmed Atlantic salmon (Salmo salar L.) | Hovda et al., 2012 |
| Gastro-intestinal tract of brown trout | Abid et al., 2013 |
| Human faeces and human gall, Cow’s milk | Björkroth et al., 2002 |
| Human vagina | Lee, 2005 |
| Human vagina | Jin et al., 2007 |
| W. confusa and W. cibaria | Canine feces | Beasley et al., 2006 |
| W. destramenae | Gut of a camel cricket | Oh et al., 2013 |
| W. helenica | Cow’s milk | Masoud et al., 2012 |
| Intestinal contents of flounder (Paralichthys olivaceus) | Cai et al., 1998 |
| W. parame- 
stenoides | Cow’s milk | Espeche et al., 2009 |
| Distal gut contents of rainbow trout fed different plant based diets | Desai et al., 2012 |
| W. vi- 
descens | Canine milk | Martin et al., 2010 |
| W. parame- 
stenoides | Midgut of Ostrinia nubilalis | Belda et al., 2011 |

2008), and a sepsis in a 48-year-old male who was operated for adenocarcinoma of the gastro-oesophageal junction and who was maintained on a total parenteral nutrition (Kumar et al., 2011). Furthermore, it also caused infection in patients with hepatocellular carcinoma occurring after liver transplant (Har- lan et al., 2011), in patients with acute lymphocytic leukemia undergoing autologous stem cell transplantation (Silvester and Dicks, 2011), and in a patient with a prosthetic joint infection (Medford et al., 2014). A large case series (i.e., a descriptive study that follows a group of patients who have a similar diagnosis or who are undergoing the same procedure over a certain period of time; http://jbjs.org/content/91/Supplement_3/21), was reported by Lee et al. (2011) and involved 10 patients with bacteremia. Risk factors for invasive infection in this group included a central line catheter insertion, a concurrent polymicrobial bacteremia and an immunocompromised host, together with gastrointestinal manipulation through endoscopy, or surgery that may have allowed the contamination of Weissella into the blood stream. Indeed, as highlighted by Medford et al. (2014), most cases of clinical infection with Weissella were associated with medical procedures within the period of infection. W. confusa was also found to cause neonatal sepsis in a foal (Lawhon et al., 2014). W. ceti has recently been recognized as the etiological agent of the so-called “weissellosis” (Welch et al., 2014), an emergent disease occurring in farmed rainbow trout (Oncorhyncus mykiss) causing septicemia with a high mortality rate (Costa et al., 2015). Weiselllosis outbreaks have been reported from commercial trout farms in the United States, China and Brazil (Liu et al., 2009; Figueiredo et al., 2012; Welch and Good, 2013; Costa et al., 2015). Symptoms of this disease include lethargy and anorexia, extensive ocular lesions, occasional cerebral hemorrhage and dark skin coloration (Welch et al., 2014). Apparently, high summer
temperatures seems to be the main predisposing factor for this emerging disease that appears to affect only the large-size fishes (0.5–1 kg) in a trout farm, while ongoing studies are focusing on ascertaining the pathogen’s route of infection and its reservoirs (Welch et al., 2014).

As suggested by several authors (Lahtinen et al., 2012; Fairfax et al., 2014; Medford et al., 2014), infections caused by Weissella, as those caused by Leuconostoc, are mainly due to their natural vancomycin resistance, and usually occur in cases of immunosuppression or underlying disease of the host. However, infections caused by Weissella spp. are generally rare, although an underestimation may occur as a result of the inability of commercial bacterial identification systems [such as the API 50 CHL kit (BioMérieux, Lyon, France) etc.] in identifying these bacteria as they closely resemble viridans streptococci (Fairfax et al., 2014).

**Potentially Probiotic or Technologically Uses of Weissella Strains**

In several studies, Weissella strains were screened for antimicrobial activity (Nam et al., 2002; Pal et al., 2010; Ndagano et al., 2011; Papagianni and Papamichael, 2011; Masuda et al., 2012; Papagianni, 2012; Vitali et al., 2012; Leong et al., 2013; Papagianni and Sergelidis, 2013; Serna-Cock et al., 2013; Yoshiyama et al., 2013; Emerenini et al., 2014). Six bacteriocins have so far been reported for Weissella strains belonging to the *W. cibaria*, *W. paramesenteroides*, and *W. hellenica* species (Table 7). Among these, the listericidal bacteriocin weissellin A was further investigated for its technological application in fermented sausages (Papagianni, 2012; Papagianni and Papamichael, 2012; Papagianni and Sergelidis, 2013), while the bacteriocinogenic *W. hellenica* strain D1501 was successfully used to enhance the shelf-life of tofu (Chen et al., 2014b).

Aiming at developing novel probiotic foods or probiotic animal feeds, many researchers have isolated and screened Weissella strains from humans (Ayeni et al., 2011; Lee et al., 2012; Gomathi et al., 2014; Zhang et al., 2014), animal feces (Cai et al., 1998; Beasley et al., 2006; Muñoz-Atienza et al., 2013) as well as from a variety of food matrices, including vegetable, fruits, cured meat and dairy matrices, for their probiotic potential (Papamanoli et al., 2003; Vitali et al., 2012; Patel et al., 2013; Yoshiyama et al., 2013; Yang et al., 2014). However, only few studies investigated the probiotic potential of Weissella strains using in vivo studies. Wang et al. (2011) demonstrated that dietary supplementation with fermented garlic together with *W. koreensis* in growing pigs can improve the average daily gain and has a positive impact on the immune response during an inflammatory challenge (Wang et al., 2011). *W. cibaria* isolates from children’s saliva were shown to inhibit *in vitro* biofilm formation and proliferation of one of the main bacterial pathogens in dental caries, especially in early-childhood caries, namely Streptococcus mutans (Kang et al., 2005). This inhibition occurred via the water soluble-polymers produced from sucrose by Weissella. Moreover, using an *in vivo* study on 72 volunteers who rinsed their teeth after brushing in the morning, afternoon and evening, with a rinse that contained the potential probiotic *W. cibaria* strain, a significant 20% reduction in plaque scores could be achieved. This indicated a high potential of *W. cibaria* isolates to inhibit biofilm formation (Kang et al., 2005). Hydrogen peroxide-producing Weissellas, belonging to the *W. cibaria* species, were also isolated from children’s saliva and were capable of inhibiting the *in vitro* production of halitosis indicators such as volatile sulfur compounds (VSC) produced by *Fusobacterium nucleatum*. Furthermore, these bacteria could inhibit the proliferation of five periodontopathic bacteria, including *F. nucleatum*. Moreover, clinical studies based on gargling with the best performing *W. cibaria* isolate resulted in a significant *in vivo* reduction of the level of VSC (Kang et al., 2006a,b). An *in vitro* antiinflammatory activity of *W. cibaria*, which consisted of inhibition of interleukin (IL)-6 and IL-8 production from human mouth epithelial cells that were originally elicited by *F. nucleatum*, could also be demonstrated *in vitro*, highlighting once again the high probiotic potential of *W. cibaria* in controlling periodontal disease (Kang et al., 2011). For all these reasons, Kang et al. (2012) successfully investigated the stability of probiotic chewing gum containing a *W. cibaria* strain.

Moon et al. (2012) demonstrated in an *in vitro* study that intracellular lipid accumulation in 3T3-L1 cells could be inhibited by the ornithine rich cytoplasmic extract of *W. koreensis* OK1-6. Lately, it was demonstrated that kimchi fermented with this *W. koreensis* strain as starter culture has an anti-obesity effect in high-fat diet-induced obese mice (Park et al., 2012).

Nevertheless, it should be considered that the current legislation on probiotics and probiotic foods/feed is very different worldwide, with a stricter regulatory framework in the European Community. Indeed, the Panel on Dietetic Products, Nutrition and Allergies of the European Food Safety Authority has rejected more than 300 health claims on the benefits of probiotic bacteria, resulting in not one of the probiotic products being allowed to claim a health benefit for the strains they contain. As a consequence, in Europe not a single probiotic product, food or supplement, can mention the health benefits of the strains it includes. Moreover, considering that the most current and accepted definition (the FAO/WHO panel definition) of probiotics define them as “live microorganisms which when being allowed to claim a health benefit for the strains they contain. As a consequence, in Europe not a single probiotic product, food or supplement, can mention the health benefits of the strains it includes. Moreover, considering that the most current and accepted definition (the FAO/WHO panel definition) of probiotics define them as “live microorganisms which when administered in adequate amounts confer a health benefit on the host” (Hill et al., 2014), even the word “probiotic” would not be allowed in the definition. These findings, together with the role as opportunistic pathogens of some weissellas and the intrinsic resistance to vancomycin and other antibiotics (Ouoba et al., 2008; Ayeni et al., 2011; Muñoz-Atienza et al., 2013), may drastically reduce the potential use of these bacteria as probiotics or even only as pre-technological (starter) bacteria in food, feed and supplements. Therefore, before thinking about using a Weissella strain for biotechnological and probiotic purposes, a thorough, strain-specific safety assessment would be mandatory.

**EPS and Prebiotics Producing Strains**

The ability to produce dextran is one of the distinctive phenotypic features of the genus Weissella (Collins et al., 1993; Björkroth and Holzapfel, 2006). In particular, strains of *W. confusa* and *W. cibaria* have received high attention in the last decade due to their ability to produce significant amounts of dextran (De
### TABLE 6 | Weissella species from human and animal clinical specimens.

| Species     | Source                                                                 | References                                                                 |
|-------------|------------------------------------------------------------------------|----------------------------------------------------------------------------|
| W. ceti     | Diseased beaked whales (Mesoplodon bidens) (muscle tissue, brain, kidney, lymph nodes, spleen of four different animals), diseased rainbow trout (Oncorhynchus mykiss) | Vela et al., 2011                                                           |
|             |                                                                        | Liu et al., 2009; Figueiredo et al., 2012                                   |
| W. cibaria  | Dog ear (otitis)                                                       | Björkroth et al., 2002                                                     |
|             | Human blood (bacteremia)                                               | Kulwichit et al., 2007                                                     |
|             | Human lung swab (bacteremia)                                           | Kulwichit et al., 2007                                                     |
|             | Human urine                                                            | Kulwichit et al., 2007                                                     |
| W. confusa  | Blood of a neonatal foal with septicemia                               | Lawhon et al., 2014                                                         |
|             | Intestine, lung, liver, and brain of a female mona monkey (Cercopithecus mona) with systemic infection | Vela et al., 2003                                                           |
|             | Human feces, Human gall, Human drain, necropsy specimens of a dog      | Björkroth et al., 2002                                                     |
|             | Human blood cultures (of patients with bacteremia)                     | Olano et al., 2001                                                         |
|             | Human feces (children)                                                 | Green et al., 1990                                                         |
|             | Human feces (of pediatric liver transplant recipients)                 | Green et al., 1991                                                         |
|             | Human peritoneal fluids (after hemicolecctomy) and abdominal walls of two patients | Riebel and Washington, 1990                                                 |
|             | Human blood (of patients with monomicrobial bacteremia)                | Kumar et al., 2011                                                         |
|             | Human blood (in an immune competent patient with underlying intramural hematomas of the aorta) | Lee et al., 2013                                                           |
|             | Human blood of 10 patients with bacteremia                             | Lee et al., 2011                                                           |
|             | Human blood cultures (of patients with infective endocarditis)         | Flaherty et al., 2003; Shin et al., 2007                                   |
|             | Purulent material from the thumb abscess of human                      | Bantar et al., 1991                                                        |
|             | Human blood (bacteremia)                                               | Harlan et al., 2011                                                        |
|             | Human blood (bacteremia)                                               | Kulwichit et al., 2007                                                     |
|             | Human bone (osteomyelitis)                                             | Kulwichit et al., 2007                                                     |
|             | Human blood from patient with bacteremia                               | Salminen et al., 2011                                                      |
|             | Human blood of two patients with bacteremia                            | Fairfax et al., 2014                                                       |
|             | Human aspirate from a knee with prosthetic joint                       | Medford et al., 2014                                                       |
| W. viridescens | Fecal DNA from celiac children                                       | Sanz et al., 2007                                                          |
|             | Human blood (bacteremia)                                               | Kulwichit et al., 2007                                                     |
| Weissella spp. | Human feces of children diagnosed with human immunodeficiency virus (HIV) | Dicks et al., 2009                                                         |

Bruyne et al., 2008, 2010; Maina et al., 2008, 2011, 2013, 2014; Björkroth et al., 2009; Katina et al., 2009; Bounaix et al., 2010; Padonou et al., 2010; Ahmed et al., 2012; Amari et al., 2013; Bejar et al., 2013; Rao and Goyal, 2013a,b; Shukla et al., 2014; Wolter et al., 2014; Tingirikari et al., 2014a,b; Malang et al., 2015), fructan and heteropolysaccharides (Tieking et al., 2003; Di Cagno et al., 2006; Malik et al., 2009; Malik, 2012; Malang et al., 2015), and novel non-digestible oligosaccharides (Chun et al., 2007; Kang et al., 2007; Patel et al., 2013; Immerzeel et al., 2014). These latter are raising interest due to their prebiotic potential, as they may (i) decrease the risk of infections and diarrhea, (ii) increase bowel function and metabolism, and (iii) pass through the gastrointestinal tract and stimulate the growth of resilient beneficial bacteria, mainly the bifidobacteria (Rastall and Gibson, 2014). Apart from their postulated health benefit, prebiotic oligosaccharides may be used in a wide range of applications in clinical, cosmetics, food and feed industries as sweeteners, humectants, possible weight controlling agents and dietary fibers (Patel and Goyal, 2011).

The dextrans produced by Weissella spp. have similar structures with mainly (ca. 97%) α-(1-6) linkages and only ca. 3% α-(1-3) linkages (Katina et al., 2009; Bounaix et al., 2010; Maina et al., 2011, 2013; Ahmed et al., 2012; Bejar et al., 2013). This makes dextran-producing strains of W. cibaria and W. confusa very appealing for a wide range of industrial applications, especially for bakery applications (Di Cagno et al., 2006; Schwab et al., 2008; Katina et al., 2009; Coda et al., 2010, 2014; Galle et al., 2010, 2012; Ruehmkorf et al., 2012; Wolter et al., 2014; Kajala et al., 2015) and for the production of cereal-based, LAB fermented functional beverages (Zannini et al., 2013).

### Isolation, Identification, Typing, and Detection

Pepe et al. (2001) differentially isolated and enumerated W. paramesenteroides on Modified Chalmers Agar on which convex colonies of 2 mm with pale-pink colonies containing a small
**TABLE 7 | Bacteriocinogenic Weissella strains, class, name, organisms against which the bacteriocins were active and relevant reference.**

| Name     | Class   | Producer organisms | Sensitive indicator strains | References |
|----------|---------|--------------------|-----------------------------|------------|
| Weissellicin 110 | Unclassified | W. cibaria 110 | Lactobacillus sakei JCM 1157, L. sanfranciscensis JCM 5668, L. homohoci JCM 1199, L. coryniformis subsp. coryniformis, JCM 1164, L. acetaotolerans JCM 3825—Weissella halotolerans JCM1114, W. kandleri JCM 5817, W. paramesenteroides JCM 9890, Leuconostoc lactis JCM 6123 | Srimonnal et al., 2007 |
| Weissellin A | Class IIA | W. paramesenteroides DX | Bacillus cereus LMG13569, Clostridium sporogenes NCTC533, C. thiamoholyticum ATCC15579, Enterococcus faecalis NCTC8176, Lactobacillus brevis ATCC8287, L. bulgaricus LMG13551, L. casei ATCC344, L. curvatus ATCC51436, L. jensenii ATCC25258, L. plantarum CECT220, L. sakei CECT9067, Lactobacillus lactis LM0230, Lact. lactis ATCC11454, Lact. lactis IL1403, Lact. lactis subsp. cremoris MGI363, Leuconostoc mesenteroides ATCC19254, Listeria innocua ATCC BAA-690D, L. monocytogenes ATCC19111, Micrococcus luteus CECT241, Pediococcus acidilactici ATCC25740, P. pentosaceus ATCC 33316, R. pentosaceus LMG13560, Staphylococcus carnosus LMG13564 | Papagian and Papamichael, 2011 |
| Weissellicin L | Unclassified | W. hellenica 4-7 | L. monocytogenes ATCC 19111, L. sakei subsp. sakei JCM 1157, L. bulgaricus ATCC 11842, W. paramesenteroides ATCC33313, W. hellenica ATCC 51523, W. vindescens ATCC 12706, S. thermophilus ATCC 19258 | Leong et al., 2013 |
| Weissellicin D | Unclassified | W. hellenica D1501 | L. lactis ssp. lactis, Lactobacillus fermentum ATCC 14931, Lb. sake, Lb. planturnant 70810, Lb. bulgaricus ATCC 7830, Lb. helveticus Mbo2-1, Lb. paracasei, Lb. curvatus, Lb. brevis, Pediococcus pentosaceus CCMCC1.2695, Streptococcus thermophilus CCMCC1.6472, Staphylococcus aureus ATCC 6538, Bacillus subtilis ATCC 6633, B. cereus ATCC 11778, Pseudomonas aeruginosa, Listeria monocytogenes CMCC 54004, Micrococcus luteus OMCC28001, Saccharomyces cerevisiae ATCC 26603, Debaryomyces Hansenii ATCC 4143, Kluyveromyces marxianus, Candida albicans CMCC 28001, Mucor circinelloides | Chen et al., 2014a |
| Weissellicin M | Unclassified | W. hellenica QU 13 | ^{a}L. lactis ssp. lactis ATCC 19435T, L. lactis ssp. lactis NCDO 497, Lactobacillus sakei ssp. sakei JCM 1157T, Lb. plantarum JCM 1149T, Weissella cibaria JCM 12495T, W. hellenica JCM 10103T, W. paramesenteroides JCM 9890T, W. confusa JCM 1093T, Pediococcus pentosaceus JCM 5885, P. dextrinicus JCM 5887T, P. acidilactici JCM 8797T, Enterococcus faecium JCM 5804T, E. durans NBRC 100479T, E. faecalis JCM 5803T, Streptococcus bovis JCM 5802T, Staphylococcus aureus ATCC 25923, Bacillus coagulans JCM 2257T, B. circulans JCM 2504T, B. subtilis ssp. subspp CCMCC 1465T, B. cereus JCM 2152T, Kocuria rhizophila NBRC 12706, Listeria innocua ATCC 33090T, Leuconostoc mesenteroides ssp. mesenteroides JCM 6124T | Masuda et al., 2012 |

^{a}Both bacteriocins were active against these bacteria but weissellicin Y showed an overall weaker activity than weissellicin M.

Fusco et al. Weissella taxonomy, ecology, and application

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Fusco et al. (2011) used an enrichment in MRS broth followed by plating on MRS agar added with 2,3,5-triphenyltetrazolium chloride (TTC), which allowed the differential isolation of LAB including several *W. confusa* and *W. cibaria* strains from sediments of a coastal marsh. However, apart from these two descriptions, there are no differential selective media available so far for isolation and enumeration of weissellas. Media for presumptive lactobacilli and leuconostocs such as MRS (De Man et al., 1960), which is generally used to cultivate weissellas, LUSM (Benkerroum et al., 1993) and SDB (Kline and Sugihara, 1971) have also been used. Due to the use of vancomycin in the LUSM medium, it may be considered the most selective and useful medium among those mentioned above, although it does not differentiate vancomycin-resistant *Leuconostoc* from weissellas. As for other lactic acid bacteria, the biochemical identification of *Weissella* species, apart from being time-consuming and labor intensive, may be uncertain or lead to misidentification, especially for species with very similar phenotypes. *Weissella* species have previously been distinguished by comparison of cellular fatty acids profiles (Samelis et al., 1998), by total soluble cell protein patterns (Dicks, 1995; Tsakalidou et al., 1997), and furthermore by biochemical-based commercial identification kits such as the RapID™ STR System (Thermo Scientific, Hudson, NH, USA), the API 50 CHL kit (BioMérieux, Lyon, France) (Lee et al., 2012), the Phoenix Automated Microbiology System (Becton Dickinson Diagnostic Systems, Sparks, MD) and the Vitek 2 system (BioMérieux, Marcy l’Etoile, France). But even these advanced tools may fail in discriminating closely related species, due to the variability and instability of phenotypic characters and the subjectivity in the interpretation of results (Graef et al., 2005; Koort et al., 2006; Shin et al., 2007; Kulwichit et al., 2008; Fusco et al., 2011; Lee et al., 2011; Fairfaxes et al., 2014;
Medford et al., 2014). Such is the case, for example, with the two closely related species *W. cibaria* and *W. confusa*, which differ in the capability of the latter to ferment galactose and xylose, while *W. cibaria* produces acid only from L-arabinose (Björkroth et al., 2002; Fusco et al., 2011). To overcome these drawbacks, molecular methods such as 16S rRNA gene sequencing (Kulwichit et al., 2008; Fairfax et al., 2014; Medford et al., 2014), amplified ribosomal DNA restriction analysis (ARDRA) (Jang et al., 2002) and ribotyping (Björkroth et al., 2002) have been used to identify and detect *Weissella* species. Schillinger et al. (2008) designed a *Weissella* and *Leuconostoc* genus specific primer set targeting in the 16S rRNA gene, while Fairfax et al. (2014) used Matrix-assisted laser desorption ionization Time-of-Flight (MALDI-TOF) to identify two *W. confusa* clinical isolates. Walter et al. (2001) designed a primer set allowing the PCR amplification of 16S rRNA gene fragments of the genera *Lactobacillus*, *Pediococcus*, *Leuconostoc*, and *Weissella*, whose separation by denaturing gradient gel electrophoresis resulted in the detection of numerous species belonging to these genera. However, it should be mentioned that, using a gel with a 32.5–40% gradient of urea and formamide increasing in the direction of electrophoresis, a co-migration of the band relevant to *W. confusa* and *Lb. reuteri* was obtained (Walter et al., 2001).

A species-specific PCR, which has been used for the identification and detection of *W. confusa* from foods and clinical specimens, has also been designed (Fusco et al., 2011). Moreover, Snyder et al. (2014) developed a conventional PCR and a quantitative PCR for identification and quantification of *W. ceti* NC36 from pure cultures and tissue samples.

The molecular typing of weissellas was achieved by numerical analysis of *HindIII* and EcoRI ribopatterns (Koert et al., 2006), repetitive element-PCR fingerprinting using (GTG)3-PCR (Boumaix et al., 2010) and fluorescent-Amplified Fragment Length Polymorphism (fAFLP) (Fusco et al., 2011). Chelo et al. (2010) analyzed genome diversity in the genera *Fructobacillus*, *Leuconostoc*, and *Weissella* by constructing physical and genetic maps, based on pulsed field gel electrophoresis (PFGE) analysis of macro-restriction fragments and hybridization of genetic markers of several strains belonging to these genera. This provided further insights into the evolution and diversification of the species of the genera *Leuconostoc*, *Oenococcus*, and *Weissella*.

**Description of Species of the Genus Weissella**

Currently, the genus *Weissella* consists of 19 species (see below). A detailed description of the currently valid described *Weissella* species is given below:

**Weissella beninensis** (Padonou et al., 2010) ben.in.en.nis.N.L.fem.adj. *beninensis*, pertaining to Benin.

*Weissella beninensis* is currently the only known motile species of *Weissella*. Motility was observed by phase contrast microscopy and peritrichous flagella could be visualized by scanning electron microscopy (Padonou et al., 2010). Clustering analysis based on 16S rRNA gene sequences showed *W. beninensis* to cluster with *W. ghanensis* as its nearest neighbor (Padonou et al., 2010), while DNA:DNA hybridization experiments showed that *W. beninensis* was a distinct species, when compared to the nearest neighbor *W. ghanensis*. Cells grow at 15°C but not at 45°C, at a pH range between 3.9 and 8.0 and in medium with 4% NaCl. Ammonia is produced from arginine and gas from glucose catabolism. Both the D and the L lactic acid enantiomers are produced as end products of glucose fermentation. Acid is produced from galactose, lactose, melibiose, raffinose and sucrose, but not from arabinose and xylose. The mol% G+C content is 37.0–37.2%.

**Weissella ceti** (Vela et al., 2011)
ceti. L. gen. n. *ceti*, of a whale.

Bacteria are short rod-shaped or cocci and non-motile. They grow in the presence of 3.0–6.5% NaCl, at pH 3.9 and 37°C, but not at 15 or 42°C (Vela et al., 2011). Both the D and the L lactic acid enantiomers are formed at a ratio of 80:20, respectively. Gas is not produced from glucose metabolism (Vela et al., 2011) which is unusual for a species of this group of organisms as these are all obligately heterofermentative and thus generally should generate gas from glucose fermentation. A 16S rRNA gene sequence analysis showed that *W. ceti* grouped together with *W. halotolerans*, *W. viridescens* and *W. minor* in a well-defined cluster (Vela et al., 2011). Hydrolysis of arginine is variable and strain dependent. Acid is produced from ribose, trehalose and maltose, but not from xylose, galactose, fructose, cellobiose, lactose, sucrose and raffinose. Dextran is not formed from sucrose and both the D and L enantiomers of lactic acid are produced. The mol% G+C content of the DNA is 39.2%. DNA:DNA hybridization was not done to confirm the novel species status of *W. ceti*, despite a high (99.5%) similarity of the 16S rRNA gene sequence to that of other *Weissella* gene sequences in the database (not specified in the publication by Vela et al., 2011).

**Weissella cibaria** Björkroth et al. (2002, p. 147Vp)
ci.ba'ri.a.L.adj. *cibaria*, pertaining to food.

*Weissella cibaria* strains originating from Thai fermented foods or from clinical samples were described by Björkroth et al. (2002). These authors noticed that a group of *W. confusa* strains possessed closely related protein fingerprinting patterns and ribotypes, but could nevertheless be distinguished into two distinct groups. These strains were investigated further using, amongst other techniques, 16S rRNA gene analyses and DNA:DNA hybridization and the novel species *W. cibaria*, which is closely related to *W. confusa*, could be distinguished. *W. cibaria* is able to grow at 15 and at 45°C, but not at 4°C (Björkroth et al., 2002). The bacteria tolerate the presence of 6.5% NaCl. *W. cibaria* strains hydrolyse arginine and produce both the D and L lactic acid enantiomer as end product of glucose fermentation. CO2 is also generated from glucose metabolism. Acid is produced from arabinose, cellobiose, salicin, sucrose and xylose, but not from galactose, lactose, melibiose, raffinose, ribose and trehalose. Dextran is formed from sucrose. The mol% G+C content of the DNA is 44–45% (Björkroth et al., 2002).
In 2002, Choi et al. described a novel species *W. kimchii* isolated from a traditional vegetable fermentation in Korea. This species was described on the basis of DNA-DNA hybridization, 16S rRNA gene phylogenetic analyses, as well as phenotypic and biochemical testing. The strain was shown to be very similar to *W. confusa*, but differing from this species on the basis of phenotypic characteristics, whole cell protein patterns and DNA-DNA hybridization data (Choi et al., 2002). The species *W. kimchii* was, however, re-classified as *W. cibaria* by Ennahar and Cai (2004), as *W. kimchii* was shown to be a later heterotypic synonym of *W. cibaria* based on 16S rRNA gene sequencing and DNA-DNA hybridization tests. The publication of Choi et al. (2002) in which *W. kimchii* was first described did not compare this species to *W. cibaria* (Björkroth et al., 2002), probably because the authors did not yet have knowledge of the *W. cibaria* species. The latter was also published in 2002, albeit at an earlier time. Therefore, given the earlier publication of the *W. cibaria* description in a work on similar bacteria, Ennahar and Cai (2004) proposed *W. kimchii* to be a later heterotypic synonym of *W. cibaria*.

**Weissella confusa** Collins et al. (1993, p. 599AL)

Synonyms: Lactobacillus *confusus* Sharpe et al. (1972, p. 396); Lactobacillus *cophrophilus* subsp. *confusus* Holzapfel and Kandler (1969, 665).

con.fu.sus.L.v. *confundere*; L. past part. *confusus* confused.

These bacteria are heterofermentative and produce both the D and L lactic acid enantiomers when fermenting glucose. Cells are short rods which tend to thicken at one end. The ability to grow at 45°C is strain dependent, with some strains showing good growth at this temperature. Ammonia results from arginine breakdown and acid is produced from cellobiose, galactose, ribose, salicin, sucrose and xylose, but not from arabinose, lactose, melibiose, raffinose and trehalose fermentation. Dextran is formed from sucrose. The mol% G+C content of the DNA is 45–47% (Collins et al., 1993).

**Weissella diestrammenae** (Oh et al., 2013)
di.es.tram.me’nae. N.L. gen. n. *diestrammenae* of Diestrammena, referring to *Diestrammenacoreana*, a camel cricket from the gut from which the bacteria were isolated.

Cells are coccoid- or rod-shaped and growth occurs from 4 to 37°C, in 0–4% (w/v) NaCl and at pH 5–8 (Oh et al., 2013). Bacteria are heterofermentative and produce gas from glucose, they are able to hydrolyse arginine and produce gas from glucose. The cell wall contains Lys-Ala-Ser and cells produce the D-enantiomer of lactic acid. The mol% G+C content of the DNA is 45% and acid is produced from mannose, acetylgulosamine, xylose and maltose but not from fructose, mannitol, and galactose. Cells are able to hydrolyse esculin and to produce ammonia from arginine (Oh et al., 2013).

**Weissella fabalis** (S nauwaert et al., 2013)
fa. bal.is. L. fem. adj. *fabalis* of or belonging to beans.

Bacteria were isolated from fermenting cocoa and 16S rRNA gene sequence analysis showed that this bacterium was most closely related to *W. fabaria* and occurred together with this species, *W. beninensis* and *W. ghanensis* in a well-separated cluster (S nauwaert et al., 2013). Cells are non-motile cocci, which produce gas from glucose in a heterofermentative metabolism. This bacteria produces the D lactic acid enantiomer, grows at 15–37°C and in the presence of 5–6% NaCl, but not in the presence of 7–8% NaCl (S nauwaert et al., 2013). Acid is formed from fructose, cellobiose, trehalose and gentiobiose, but not from arabinose, ribose, xylose, galactose, lactose, melibiose, sucrose and raffinose. Arginine is hydrolyzed. The mol% G+C content is 37% (S nauwaert et al., 2013).

**Weissella fabaria** (De Bruyne et al., 2010)
fa. ba.ri.a. L. fem. adj. *fabaria*, of or belonging to beans.

Bacteria were also isolated from fermenting cocoa and are heterofermentative producing CO₂ from glucose metabolism. They furthermore produce both the D and L lactate enantiomer in an approximate 90:10 ratio, respectively (De Bruyne et al., 2010). Cells are non-motile, cocoid with growth occurring at 15–37°C and at pH 5.0–9.0. No growth occurred in the presence of 5% NaCl. *W. fabaria* hydrolyses arginine and acid is produced from fructose, mannose, cellobiose, trehalose and gentiobiose, but not from arabinose, ribose, raffinose, sucrose, xylose, galactose, lactose, and melibiose. According to a 16S rRNA gene sequence analysis, *W. fabaria* was shown to be closely related to *W. ghanensis* and occurred together with this species, as well as with *W. fabalis* and *W. beninensis* in a well-delineated cluster (De Bruyne et al., 2010; S nauwaert et al., 2013; Björkroth et al., 2014). The mol% G+C content of the DNA is 38.2% (De Bruyne et al., 2010).

**Weissella ghanensis** (De Bruyne et al., 2008)
gha.nen’sis. N.L. fem. adj. *ghanensis*, pertaining to Ghana.

*Weissella ghanensis* was also isolated from fermenting cocoa. These bacteria are small rods, appearing singly or in chains and are non-motile. *W. ghanensis* grows at 15–37°C, but similar to *W. fabaria*, it does not grow in the presence of 5% NaCl (De Bruyne et al., 2008). The strain produces gas (CO₂) from glucose fermentation, with both the D and L lactic acid enantiomers being produced at a ratio of approx. 90:10 or 95:5, respectively, depending on the strain (De Bruyne et al., 2008). *W. ghanensis* hydrolyses esculin and produces ammonia from arginine. Acid is produced from cellobiose, fructose, maltose, salicin and trehalose, with no acid being produced from arabinose, galactose, melibiose, raffinose, ribose and xylose. The mol% G+C content of the DNA is 40%.

**Weissella halotolerans** Collins et al. (1993, p. 599VF)

Synonym: Lactobacillus *halotolerans* Kandler et al. (1983). (p. 672). Effective publication: Kandler et al. (1983); Kandler et al. (p. 283).
Weissella halotolerans was originally described as “Lactobacillus viridescens subsp. halotolerans” by Reuter (1970), but this name was not on the Approved List of Bacterial Names of Skerman et al. (1989). “Lactobacillus halotolerans” was subsequently described by Kandler et al. (1983) as irregular short, even coccoid rods with rounded ends and with a tendency to form coiling chains and lumping together. Growth of these bacteria occurred between 10 and 40°C, with good growth occurred only from 12°C. Very weak growth could be demonstrated at 14% NaCl. “L. halotolerans” was shown to ferment fructose, glucose, gluconate, maltose, mannose, ribose and trehalose, but not cellobiose, galactose, lactose, mannitol, melilizite, melibiose, raffinose, rhamnose, sorbitol, sucrose, xylose and esculin. The cell wall murein type was Lys-Ala-Ser and the mol% G+C content of the DNA was 45% (Kandler et al., 1983). Some 10 years later, Collins et al. (1993) finally reclassified “Lactobacillus halotolerans” as Weissella halotolerans.

**Weissella hellenica** Collins et al. (1993, p. 601)

**Weissella koreensis** Lee et al. (2002). (p. 1260)

**Weissella minor** Collins et al. (1993, p. 599)

**Weissella oryzae** (Tohno et al., 2013)

Bacteria are non-motile and of spherical, but sometimes lenticular shape, usually occurring in pairs or short chains, with a tendency to form clusters (Collins et al., 1993). Cells grow at 10°C, show delayed growth at 4°C and do not grow at 37°C. The bacteria are heterofermentative but gas production is poor. The cells produce predominantly (>98%) D-lactate, they do not hydrolyse arginine. Growth occurs at 8% but not at 10% NaCl, or in medium at pH 4.8–5.0. They are Vogues-Proskauer negative. Acid is produced from glucose, fructose, mannose, maltose, trehalose but not from ribose, xylose, rhamnose, mannitol, cellobiose, lactose, melilizite and raffinose. The cell wall peptidoglycan belongs to the Lys-Ala-Ser(Ala)- type and the G+C content of the DNA was reported to range from 39.4 to 40 mol% (Collins et al., 1993).

**Weissella kandleri** Collins et al. (1993, p. 599)

**Weissella koreensis** Lee et al. (2002). (p. 1260)

W. koreensis was isolated from Korean kimchi and is most closely related to W. kandleri on basis of a 16S rRNA gene nucleotide analysis. W. koreensis bacteria are not motile and the cells are irregular, short and rod-shaped or coccoid. These bacteria were able to grow at 10 and 37°C but not at 42°C. Cells also grew in a pH range of pH 4.0–8.0, but not in the presence of 8 or 10% NaCl. Arginin was hydrolysed and acid was produced from arabinose, ribose and xylose, but not from cellobiose, galactose, maltose, melilizite, raffinose, sucrose or trehalose. The bacteria form exclusively the D lactic acid enantiomer. The cell wall was shown to contain Lys-Ala-Ser and the mol% G+C content of the DNA was 37 mol% (Lee et al., 2002).

**Weissella minor** Collins et al. (1993, p. 599)

Synonyms: *Lactobacillus minor* Kandler et al. (1983). (p. 672). Effective publication: Kandler et al. (1983). (p. 284) (*Lactobacillus corynoides* subsp. minor) Abo-Elnaga and Kandler (1965) (p. 128); *Lactobacillus viridescens* subsp. minor Kandler and Abo-Elnaga (1966) (p. 754).

W. minor was previously classified as a subspecies of *Lactobacillus viridescens*, i.e., *L. viridescens* subsp. *minor* (Abo-Elnaga and Kandler, 1965), similar to the case of *W. halotolerans* which was previously classified as *Lactobacillus viridescens* subsp. *halotolerans* (Reuter, 1970; Kandler et al., 1983). These bacteria were re-classified to “Lactobacillus minor” by Kandler et al. (1983) who described these bacteria as occurring as irregular, short rods with rounded to tapered ends, often bent and with unilateral swelling. Bacteria were non-motile and were able to grow between 10 and 40°C. Good growth could be shown to occur up to 8% NaCl, and very weak growth at 10% NaCl. Nitrate was not reduced to nitrite, the cell wall contained murein of the Lys-Ser-Ala type and the mol% G+C content of the DNA was 44 mol%. The bacteria were able to produce acid from cellobiose, fructose, glucose, maltose, mannose, melilizite, ribose, sucrose, trehalose and esculin, but not from arabinose, galactose, lactose, mannitol, melilizite, raffinose, rhamnose, sorbitol, and xylose (Kandler et al., 1983).

**Weissella oryzae** (Tohno et al., 2013)

W. oryzae was isolated from fermented rice grains were irregular, short rod-shaped or coccoid and occurred singly or in pairs or short chains. Cells grew at 10–42°C, but not at 4 or 50°C. Growth also occurred at pH 3.9–9.0 and with 4.0–6.5% NaCl, but not with 8% NaCl (Tohno et al., 2013). The cell wall peptidoglycan contains glutamic acid, lysine, serine and alanine and acid was produced from arabinose, ribose, xylose, galactose (delayed reaction), glucose, fructose, mannose, maltose, melilizite, trehalose and glucanate. Acid was not generated from arabinose, xylose, sorbose, rhamnose, dulcitol, inositol, mannitol, esculin, cellobiose, lactose,
sucrose, melizitose, and raffinose. Esculin was not hydrolyzed, arginine hydrolysis was positive. Only the Dlactic acid enantiomer was formed from carbohydrate fermentation. The mol% G+C content of the DNA was 40.6 mol%.

**Weissella paramesenteroides** (Garvie, 1967; Collins et al., 1993) comb. nov.
Gr. prep. para, beside; N.L. fem. adj. mesenteroides, a specific epithet; N.L. fem. adj. *paramesenteroides*, beside *Leuconostoc mesenteroides*.

*Weissella paramesenteroides* was proposed as a new species of the genus *Leuconostoc* by Garvie in 1967 based on differences to the closely related *Leuconostoc mesenteroides* regarding amino acid and vitamin requirements, and the failure to hydrolyze esculin and salicin. Morphologically, these bacteria are very similar to *L. mesenteroides* and do not form dextran from sucrose (Garvie, 1967) or ammonia from arginine. They are more tolerant toward NaCl than *L. mesenteroides* and can grow in media with an initial pH below 5. The optimum growth temperature is 18–24°C, but many strains also grow at 30°C. The bacteria produce acid from galactose, maltose, melibiose, sucrose and trehalose. The peptidoglycan type is Lys-Ala or Lys-Ser-Ala and the G+C content of the DNA is 37–38 mol%. Based on 16S rRNA gene sequencing analysis, the leuconostocs were shown to comprise three distinct lineages of which the "*L. paramesenteroides*" group (including the species formerly known as "*L. confusus, L. minor, L. kandleri, L. halotolerans,* and "*L. viridescens*") were re-assigned to the genus *Weissella* by Collins et al. (1993). The re-classification of this new group included the new species *W. paramesenteroides* (Collins et al., 1993).

**Weissella soli** (Magnusson et al., 2002)
so’li.L.n. solum soil; L.gen.n.soli of the soil.

*W. soli* was isolated from garden soil in Uppsala, Sweden. Bacteria are non-motile rods that are thickened at one end and occurred singly or in pairs. The lactic acid enantiomer was produced mainly D-lactic acid. Growth occurred between 4 and 40°C, but not at 42°C. Acid was produced from ribose, D-xylose, glucose, mannose, maltose, melibiose, sucrose, trehalose and raffinose, but not from L-xylose, galactose, fructose, rhamnose, mannitol, cellobiose, lactose, and melizitose. Esculin was shown to be hydrolyzed and arginine was cleaved. The G+C content of the DNA was 43% mol (Magnusson et al., 2002).

**Weissella thailandensis** (Tanasupawat et al., 2000)
thai.lan.den.sis.M.L.fem. adj. *thailandensis* pertaining to Thailand, where the strains were first isolated.

*W. thailandensis* was isolated from fermented fish (pla-ra) in Thailand and cells were non-motile and coccus-shaped. These bacteria did not reduce nitrate and did not hydrolyze arginine, esculin, gelatin or starch. The bacteria were able to grow in 10% NaCl, at temperatures of 25–37°C but not at 42°C. Growth also occurred at pH 8.0, while no growth could be observed at pH 4.5 or pH 8.5. Acid was produced from ribose, arabinose, fructose, galactose, mannose, maltose, melibiose, raffinose, and rhamnose, but not from cellobiose, mannitol, melizitose, sorbitol or xylose. The cell wall contains Lys-Ala; and the mol% G+C content in the DNA was found to range from 38 to 41.2 (Tanasupawat et al., 2000).

**Weissella uvarum** Nisiotou et al., 2014
u.va.rum.L.fem. gen. pl. n. *uvarum* of grapes, where the type strain was isolated.

This bacterium was isolated from grapes from Nemea in Greece. The cells were non-motile short rods, or showed coccoid morphology. The cells were able to grow at 15 and 42°C, but not at 4 or 45°C. Cells were not capable of growth at pH 3.9 or in the presence of 6.5% NaCl, but could grow at pH 8.0 and in the presence of 4% NaCl. Ammonia was produced from arginine and acid was produced from ribose, glucose, fructose, mannose, trehalose, melizitose, but not from glycerol, arabinose, xylose, galactose, rhamnose, mannitol, sorbitol, esculin, cellobiose, maltose, lactose, melibiose, sucrose, and raffinose (Nisiotou et al., 2014). The mol% G+C content of the DNA and amino acid composition of the cell wall were not yet determined.

**Weissella viridescens** (Niven and Evans., 1957; Collins et al., 1993) comb. nov.
vi ri.des’cens. M. L. pres. part. *viridescens*, growing green, greening.

The bacteria previously known as *Lactobacillus viridescens* were re-classified as *Weissella viridescens* by Collins et al. (1993). Cells are small rods, which occur either singly or in pairs, and the ends of the rods appear slightly tapered. Nitrate is not reduced and sodium hippurate, esculin, arginine and starch are not hydrolyzed. Growth occurs in the presence of 6.5% NaCl and at the low temperature of 5°C, but not at 45°C. These bacteria ferment glucose, mannose, fructose and maltose, but no acid is produced from xylose, arabinose, galactose, lactose, raffinose or sorbitol (Niven and Evans, 1957). The interpeptide bridge of the peptidoglycan is composed of Lys-Ala-Ser. The mol% G+C of the DNA is 41–44 (Kandler and Weiss, 1986). Some strains produce large amounts of dextran from sucrose fermentation, a trait that may be lost rapidly in stock cultures (Niven and Evans, 1957).

**Conclusions**

The genus *Weissella* is a well-delineated genus within the family *Leuconostocaceae* and contains 19 validly described species. *Weissella* species are generally difficult to distinguish from other heterofermentative cocci such as leuconostocs, or rod-shaped bacteria such as certain *Lactobacillus* strains on the basis of phenotypic or biochemical properties alone. An accurate species identification thus is generally only possible using molecular biological methods, such as sequencing of 16S rRNA or other house-keeping genes, DNA:DNA hybridization and by typing methods such as rep-PCR or fAFLP. Weissella occur in a great variety of habitats, including the skin, milk and feces of animals, the saliva, breast milk, feces and vagina of humans, on plants and
veggies, as well as in a variety of fermented foods such as Euro-

Abid, A., Davies, S. J., Waines, P., Emery, M., Castex, M., Gioacchini, G., et al. (2013). Dietary symbiotic application modulates Atlantic salmon (Salmo

Albeshrat, R., Ehrmann, M. A., Korakli, M., Yazaji, S., and Vogel, R. F. (2011). Phenotypic and genotypic analyses of lactic acid bacteria in local fermented

Amari, M., Arango, L. F., Gabriel, V., Robert, H., Morel, S., Moulis, C., et al. (2011). Evaluation of the functional potential of

Amare, A., Siddiqi, K., Arman, M., and Ahmed, N. (2012). Characterization of high molecular weight dextran produced by Weissella cibaria CCMGD3X.

Ampe, F., ben Omar, N., Moizan, C., Wacher, C., and Guyot, J.-P. (1999). Polyphas-

Aquilanti, L., Silvestri, G., Zannini, E., Osimani, A., Santarelli, S., and Clementi, F.

Ayeni, F. A., Sánchez, B., Adeniyi, B. A., de Los Reyes-Gavilán, C. G., Margolles, A., and Ruas-Madiedo, P. (2011). Evaluation of the functional potential of

Bae, S., Fleet, G. H., and Heard, G. M. (2006). Lactic acid bacteria associated with wine grapes from several Australian vineyards. J. Appl. Microbiol. 100, 712–727.

doi: 10.1111/j.1365-2672.2006.02890.x

Banta, C. E., Relloso, S., Castell, F. R., Smayevsky, J., and Bianchini, H. M. (1991). Abscess caused by vancomycin-resistant Lactobacillus confusus. J. Clin.

Beasley, S. S., Manninen, T. J., and Saris, P. E. (2006). Lactic acid bacteria iso-

Beijerinck. II. Das Subgenus Weissella, sp. TN610 with

Beldel, E., Pedrola, L., Peretó, J., Martínez-Blanch, J. F., Montagud, A., Navarro, E., et al. (2011). Microbial diversity in the midguts of field and lab-reared popula-

Benchaalal, D., Bounaix, M. S., Robert, H., Gabriel, V., Morel, S., Remaud-Siméon, M., Gabriel, N., Misbah, M., Sandine, W. E., and Elaraki, A. T. (1993). Devel-

Björkroth, K. A., J. Dicks, L. M. T. D., and Endo, A. (2014). “The genus Weissella,” in Lactic Acid Bacteria, Biodiversity and Taxonomy, eds W. H. Holzapfel and B. J. Wood (Chichester: Wiley Blackwell), 418–428.

Björkroth, K. A., J. Dicks, L. M. T. D., and Holzapfel, W. H. (2009). “Genus III. Weissella Collins, Samelis, Metaxopoulos and Wallbanks 1994, 370V (Effect-

Birkofer, C., Applied Environ Microbiol. 59, 607–609.

Birkofer, C., J. Dicks, L. M. T. D., and Holzapfel, W. H. (2006). “Genera Leuconostoc, Oenococcus and Weissella,” in The Prokraryotes, eds M. Dworkin, S. Falkow, E. Rosenberg, K. Schleifer, and E. Staekebrandt (New York, NY: Springer), 267–319.

Birkofer, C., K. J., Schillinger, U., Geisen, R., Weiss, N., Hoste, B., Holzapfel, W. H., et al. (2002). Taxonomic study of Weissella confusa and description of Weissella cibaria sp. nov., detected in food and clinical samples. Int. J. Syst. Evol. Microbiol. 52, 141–148.

Bounaix, M. S., Robert, H., Gabriel, V., Morel, S., Remaud-Siméon, M., Gabriel, B., et al. (2010). Characterization of dextran-producing Weissella strains iso-

Bourjou, C., Pedrola, L., Peretó, J., Martínez-Blanch, J. F., Montagud, A., Navarro, E., et al. (2011). Microbial diversity in the midguts of field and lab-reared popula-

Boudjouk, M., Sandine, W. E., and Elaraki, A. T. (1993). Development and use of a selective medium for isolation of Weissella species, e.g., of Weissella viridescens.

Bouza, E., Pedrola, L., Peretó, J., Martínez-Blanch, J. F., Montagud, A., Navarro, E., et al. (2011). Microbial diversity in the midguts of field and lab-reared popula-

Boudjouk, M., Sandine, W. E., and Elaraki, A. T. (1993). Development and use of a selective medium for isolation of Weissella species, e.g., of Weissella viridescens.

Bouza, E., Pedrola, L., Peretó, J., Martínez-Blanch, J. F., Montagud, A., Navarro, E., et al. (2011). Microbial diversity in the midguts of field and lab-reared popula-

Boudjouk, M., Sandine, W. E., and Elaraki, A. T. (1993). Development and use of a selective medium for isolation of Weissella species, e.g., of Weissella viridescens.

Boudjouk, M., Sandine, W. E., and Elaraki, A. T. (1993). Development and use of a selective medium for isolation of Weissella species, e.g., of Weissella viridescens.

Boudjouk, M., Sandine, W. E., and Elaraki, A. T. (1993). Development and use of a selective medium for isolation of Weissella species, e.g., of Weissella viridescens.

Boudjouk, M., Sandine, W. E., and Elaraki, A. T. (1993). Development and use of a selective medium for isolation of Weissella species, e.g., of Weissella viridescens.

Boudjouk, M., Sandine, W. E., and Elaraki, A. T. (1993). Development and use of a selective medium for isolation of Weissella species, e.g., of Weissella viridescens.

Boudjouk, M., Sandine, W. E., and Elaraki, A. T. (1993). Development and use of a selective medium for isolation of Weissella species, e.g., of Weissella viridescens.

Boudjouk, M., Sandine, W. E., and Elaraki, A. T. (1993). Development and use of a selective medium for isolation of Weissella species, e.g., of Weissella viridescens.

Boudjouk, M., Sandine, W. E., and Elaraki, A. T. (1993). Development and use of a selective medium for isolation of Weissella species, e.g., of Weissella viridescens.
mustard products of Taiwan. Int. J. Food Microbiol. 135, 203–210. doi: 10.1016/j.ijfoodmicro.2009.07.032

Chelo, I. M., Zé-Zé, L., and Tenreiro, R. (2010). Genome diversity in the genera Fructobacillus, Leuconostoc and Weissella determined by physical and genetic mapping. Microbiology 156, 420–430. doi: 10.1099/mic.0.034308-0

Chen, C., Chen, X., Jiang, M., Rui, X., Li, W., and Dong, M. (2014a). A newly discovered bacteriocin from Weissella hellenica D1501 associated with Chinese Dong fermented meat (Nanx Wudil. Food Control 42, 116–124. doi: 10.1016/j.foodcont.2014.01.031

Chen, C., Rui, X., Lu, Z., Li, W., and Dong, M. (2014b). Enhanced shelf-life of tofu by using bacteriocinogenic Weissella hellenica D1501 as bioprotective cultures. Food Control 46, 203–209. doi: 10.1016/j.foodcont.2014.05.004

Chen, Y. S., Wu, H. C., Lo, H. Y., Lin, W. C., Hsu, W. H., Lin, C. W., et al. (2012). Isolation and characterisation of lactic acid bacteria from jiang-gua (fermented cucumbers), a traditional fermented food in Taiwan. J. Sci. Food Agric. 92, 2096–2079. doi: 10.1002/jsfa.5583

Chen, Y. S., Yanagida, F., and Shinohara, T. (2005). Isolation and identification of lactic acid bacteria from soil using an enrichment procedure. Lett. Appl. Microbiol. 40, 195–200. doi: 10.1111/j.1365-2672.2005.01653.x

Cho, J., Lee, D., Yang, C., Jeon, J., Kim, J., and Han, H. (2006). Microbial population dynamics of kimchi, a fermented cabbage product. FEMS Microbiol. Lett. 257, 262–267. doi: 10.1111/j.1574-6968.2006.00816.x

Cho, K. T., Richardson, M. M., Kirkbride, P. K., McNevin, D., Nelson, M., Pianca, D., et al. (2014). Recovery and identification of bacterial DNA from illicit drugs. Forensic Sci. Int. 235, 79–85. doi: 10.1016/j.forsciint.2013.12.006

Choi, H. J., Cheigh, C. I., Kim, S. B., Lee, J. C., Lee, D. W., Choi, S. W., et al. (2002). Weissella kimchii sp. nov., a novel lactic acid bacterium from kimchi. Int. J. Syst. Evol. Microbiol. 52, 507–511. doi: 10.1099/ijs.0.01957-0

Chun, J., Kim, G. M., Lee, K. W., Kwon, G. H., Park, J. Y., et al. (2007). Conversion of isoflavone glucosides to aglycones in soymilk by fermentation with lactic acid bacteria. J. Food Sci. 72, M39–M44. doi: 10.1111/j.1750-3841.2007.00276.x

Cocolin, L., Dolci, P., Rantsiou, K., Urso, R., Cantonii, C., and Comi, G. (2009). Lactic acid bacteria ecology of three traditional fermented sausages produced in the North of Italy as determined by molecular methods. Meat Sci. 82, 125–132. doi: 10.1016/j.meatsci.2009.01.004

Coda, R., Di Cagno, R., Gobbetti, M., and Rizzello, C. G. (2014). Sourdough lactic acid bacteria: exploration of non-wheat cereal-based fermentation. Food Microbiol. 37, 51–58. doi: 10.1016/j.fm.2013.06.018

Coda, R., Nionelli, L., Rizzello, C. G., De Angelis, M., Tossut, P., and Gobbetti, M. (2010). Spelt and emmer flours: characterization of the lactic acid bacteria species. Int. J. Food Microbiol. 130, 108–116. doi: 10.1016/j.ijfoodmicro.2009.01.019

Coda, R., Di Cagno, R., Gobbetti, M., and Rizzello, C. G. (2014). Characterization of Leuconostoc species of the Leuconostoc sensu stricto line of descent, Leuconostoc oenos and Weissella paramesenteroides revealed by numerical analysis of total soluble cell protein patterns. Syst. Appl. Microbiol. 38, 99–102. doi: 10.1016/S0723-2020(11)80455-8

Dicks, L. M., Fraser, T., ten Doeschate, K., and van Reenen, C. A. (2009). Recovery and identification of bacterial DNA from illicit drugs. Forensic Sci. Int. 190, 220–228. doi: 10.1016/j.forsciint.2008.07.010

Dick, M., Fraser, T., ten Doeschate, K., and van Reenen, C. A. (2009). Microbial, sensory and volatile changes during the anaerobic cold storage of morcilla de Burgos previsouly inoculated with Weissella viridescens and Leuconostoc mesenteroides. Int. J. Food Microbiol. 131, 168–177. doi: 10.1016/j.ijfoodmicro.2009.02.019

Elavarasi, V., Pugazhendhi, A., Poornima Priyadharansi, T. K., Valsala, H., and Thamaraiselvi, K. (2014). Screening and characterization of Weissella cibaria isolated from food source for probiotic properties. Int. Comp. Appl. 1, 29–32. doi: 10.1016/j.sfj.2013.08.013

Diez, A. M., Björkroth, J., Jaime, L. and Rovira, J. (2009). Microbial, sensory and volatile changes during the anaerobic cold storage of morcilla de Burgos previously inoculated with Weissella viridescens and Leuconostoc mesenteroides. Int. J. Food Microbiol. 131, 168–177. doi: 10.1016/j.ijfoodmicro.2009.02.019

Endo, A., Futagawa-Endo, Y., Kawasaki, S., Dicks, L. M. T., Niiyama, Y., and Okada, S. (2009). Sodium acetate enhances hydrogen peroxide production in Weissella cibaria. Lett. Appl. Microbiol. 49, 136–141. doi: 10.1111/j.1742-7965.2009.02633.x

Ennahar, S., and Cai, Y. (2004). Genetic evidence that Weissella kimchii Choi et al. 2002 is a later heterotypic synonym of Weissella cibaria Björkroth et al. 2002. Int. J. Syst. Evol. Microbiol. 54, 463–465. doi: 10.1099/ijs.0.02783-0

Espuche, M. C., Otero, M. C., Sesma, F., and Nader-Macias, M. E. (2009). Screening of surface properties and antagonistic substances production by lactic acid bacteria isolated from the mammary gland of healthy and mastitic cows. Vet. Microbiol. 135, 346–357. doi: 10.1016/j.vetmic.2008.09.078

Fairfax, M. R., Lephart, P. R., and Salimnia, H. (2014). Weissella confusa: problems with identification of an opportunistic pathogen that has been found in fermented foods and proposed as a probiotic. Front. Microbiol. 5:254. doi: 10.3389/fmicb.2014.00254

Figuereido, H. C., Costa, F. A., Leal, C. A., Carvalho-Castro, G. A., and Leite, R. C. (2012). Weissella sp. outbreaks in commercial rainbow trout

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Weissella taxonomy, ecology, and application

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Weissella taxonomy, ecology, and application
(Oncorhynchus mykiss) farms in Brazil. Vet. Microbiol. 156, 359–366. doi: 10.1016/j.vetmic.2011.11.008
Flaherty, J. D., Levett, P. N., Dewhurst, F. E., Troe, T. E., Warren, J. R., and Johnson, S. (2003). Fatal case of endocarditis due to Weissella confusa. J. Clin. Microbiol. 41, 2237–2239. doi: 10.1128/JCM.41.5.2237-2239.2003
Fuka, M. M., Wallisch, S., Engel, M., Welzl, G., Havrankel, J., and Schlote, M. (2013). Dynamics of bacterial communities during the ripening process of different Croatian cheese types derived from raw ewe’s milk cheeses. PLoS ONE 8:e80734. doi: 10.1371/journal.pone.0080734
Fusco et al. Weissella taxonomy, ecology, and application
Kim, T. W., Lee, J. H., Kim, S. E., Park, M. H., Chang, H. C., and Kim, H. Y. (2009). Analysis of microbial communities in doenjang, a Korean fermented soybean paste, using nested PCR-denaturing gradient gel electrophoresis. *Int. J. Food Microbiol.* 131, 265–271. doi: 10.1016/j.ijfoodmicro.2009.03.001

Kline, L., and Sugihara, T. F. (1971). Microorganisms of the San Francisco sourdough process. II. Isolation and characterization of undiscribed bacterial species responsible for souring activity. *Appl. Microbiol.* 21, 459–465.

Koort, J., Coenye, T., Santos, E. M., Molinero, C., Jaime, I., Rovira, J., et al. (2006). Diversity of *Weissella viridescens* strains associated with “Morcella de Burgos.” *Int. J. Food Microbiol.* 109, 164–168. doi: 10.1016/j.ijfoodmicro.2006.01.024

Kopermsuba, P., and Yunchalard, S. (2010). Identification of lactic acid bacteria associated with the production of pla-a-som, a traditional fermented fish product of Thailand. *Int. J. Food Microbiol.* 138, 200–204. doi: 10.1016/j.ijfoodmicro.2010.01.024

Korkeala, H., and Björkroth, K. J. (1997). Spoilage and contamination of vacuum packaged cooked sausages: a review. *J. Food Prot.* 60, 724–731.

Kostinek, M., Specht, I., Edward, V. A., Schillinger, U., Hertel, C., Holzapfel, W. H., et al. (2005). Diversity and technological properties of predominant lactic acid bacteria from fermenting cassava for selection as starter cultures. *Int. J. Food Microbiol.* 114, 342–351. doi: 10.1016/j.ijfoodmicro.2006.09.029

Kostinek, M., Specht, I., Edward, V. A., Schillinger, U., Hertel, C., Holzapfel, W. H., et al. (2005). Diversity and technological properties of predominant lactic acid bacteria from fermenting cassava used for the preparation of Gari, a traditional African food. *Syst. Appl. Microbiol.* 28, 527–540. doi: 10.1016/j.syapm.2005.03.001

Kulwichit, W., Nilgate, S., Chatsuwan, T., Krajiw, S., Unhasuta, C., and Chongthansattra, P., and Yunchalard, S. (2010). Identification of lactic acid bacteria from fermented cassava used for the preparation of Gari, a traditional African food. *Syst. Appl. Microbiol.* 33, 259–271. doi: 10.1016/j.syapm.2010.01.024

Kulwichit, W., Nilgate, S., Krajiw, S., Unhasuta, C., and Chongthansattra, P., and Yunchalard, S. (2010). Identification of lactic acid bacteria from fermented cassava used for the preparation of Gari, a traditional African food. *Syst. Appl. Microbiol.* 33, 259–271. doi: 10.1016/j.syapm.2010.01.024

Lee, M. R., Huang, Y. T., Liao, C. H., Lai, C. C., Lee, P. I., and Hueh, P. R. (2002). Probiotic properties of *Weissella confusa* sp. nov., isolated from kimchi. *Weissella* sp. nov., isolated from kimchi. *Anaerobe* 8, 183–190. doi: 10.1006/anab.2001.0228

Lee, J. S., Lee, K. C., Ahn, J. S., Mheen, T. I., Pyun, Y. R., and Park, Y. H. (2002). Identification and evaluation of the probiotic potential of *Weissella koreensis* sp. nov., a lactic acid bacterium isolated from soil. *Int. J. Syst. Evol. Microbiol.* 52, 831–834. doi: 10.1099/ijs.0.02150-0

Maina, N. H., Juvenon, M., Domingues, R. M., Virkki, L., Jokela, J., and Tenkainen, M. (2013). Structural analysis of linear mixed-linkage glucooligosaccharides by tandem mass spectrometry. *Food Chem.* 136, 1496–1507. doi: 10.1016/j.foodchem.2012.09.075

Makarova, K., Sleasarev, A., Wolf, Y., Sorokin, A., Mirkin, B., Koonin, E., et al. (2006). Comparative genomics of the lactic acid bacteria. *Proc. Natl. Acad. Sci. U.S.A.* 103, 15611–15616. doi: 10.1073/pnas.0607171103

Malang, S. K., Maina, N. H., Schwab, C., Tenkainen, M., and Lacroix, C. (2015). Characterization of exopolysaccharide and ropy capsular polysaccharide formation by *Weissella*. *Food Microbiol.* 46, 418–427. doi: 10.1016/j.fm.2014.08.022

Malik, A. (2012). Molecular cloning and in silico characterization of fractansucrase gene from *Weissella confusa* MBFENG-21 isolated from local brewer. *Asia-Pacific J. Mol. Biol. Biotechnol.* 20, 33–42. Available online at: http://www.myjurnal.my/public/article-view.php?id=6264

Martín, R., Olivares, M., Pérez, M., Xaus, J., Torre, C., Fernández, L., et al. (2012). Diversity of the *Weissella* strains from soya. *FEMS Microbiol. Lett.* 300, 131–138. doi: 10.1016/j.femsle.2010.07.002

Martín, R., Heilig, H. G., Zoetendal, E. G., Jiménez, E., Fernández, L., Smidt, H., et al. (2007a). Cultivation-independent assessment of the bacterial diversity of breast milk among healthy women. *Res. Microbiol.* 158, 31–37. doi: 10.1016/j.resmic.2006.11.004

Martín, R., Heilig, H. G., Zoetendal, E. G., Fernández, L., Smidt, H., et al. (2007b). Diversity of the *Lactobacillus* group in breast milk and vagina of healthy women and potential role in the colonization of the infant gut. *J. Appl. Microbiol.* 103, 2638–2644. doi: 10.1111/j.1365-2672.2007.03497.x

Martín, R., Olivares, M., Pérez, M., Xaus, J., Torre, C., Fernández, L., et al. (2010). Identification and evaluation of the probiotic potential of lactobacilli isolated from canine milk. * Vet. J.* 185, 193–198. doi: 10.1016/j.tvjl.2009.04.014

Mas, M., Tabla, R., Moriche, J., Roa, I., Gonzalez, J., Rebollo, J. E., et al. (2002). Ibores goat’s milk cheese: microbiological and physicochemical changes throughout ripening. *Le Lait* 82, 579–587. doi: 10.1051/la:2002034

Masoud, W., Vogensen, F. K., Lillevang, S., Abu Al-Soud, W., Sørensen, S. J., and Jakobsen, M. (2012). The fate of indigenous microbiota, starter cultures, *Esherichia coli*, *Listeria innocua* and *Staphylococcus aureus* in Danish raw milk and cheeses determined by pyrosequencing and quantitative real-time (qRT)-PCR. *Int. J. Food Microbiol.* 153, 192–202. doi: 10.1016/j.fmb.2011.11.014
Masuda, Y., Zendo, T., Sawa, N., Perez, R. H., Nakayama, J., and Sonomoto, K. (2012). Characterization and identification of weissiellin Y and weissiellin M, novel bacteriocins produced by Weissella helenica QU 13. J. Appl. Microbiol. 112, 99–108. doi: 10.1111/j.1365-2672.2011.05180.x

Mathara, J. M., Schilling, U., Kutima, P. M., Mbogu, S. K., and Holzapfel, W. H. (2004). Isolation, identification and characterization of the dominant microorganisms of kulenao: The Maasai traditional fermented milk in Kenya. Int. J. Food Microbiol. 94, 269–278. doi: 10.1016/j.ijfoodmicro.2004.01.008

Medford, R., Patel, S. N., and Evans, G. A. (2014). A confusing case—Weissella confusa prosthetic joint infection: a case report and review of the literature. Can. J. Infect. Dis. Med. Microbiol. 25, 173–175.

Merivirta, L. O., Koort, J. M., Kivisaari, M., Korkeala, H., and Björkroth, K. (2004). Antifungal activity of 2 lactic acid bacteria of the genus isolated from the gut of a camel (Camelus dromedarius). World J. Microbiol. Biotechnol. 20, 118, 520–525. doi: 10.1111/j.1574-6968.2004.00292-9

Moon, Y. J., Lei, V., and Jensen, L. B. (2008). Resistance of potential probiotic lactic acid bacteria and bifidobacteria of African and European origin to antimicrobials, determination and transferability of the resistance genes to other bacteria. Int. J. Food. Microbiol. 121, 217–224. doi: 10.1016/j.ijfoodmicro.2007.11.018

Nam, H., Whang, K., and Lee, Y. (2007). Analysis of vaginal lactic acid producing bacteria and fermentation characteristics of togwa, a Tanzanian fermented food. Food Microbiol. 24, 123–129. doi: 10.1016/j.fm.2006.09.002

Oh, S. J., Shin, J. H., Lee, D. W., Song, J. C., Suh, H. J., Chang, U. J., et al. (2010). Identification of lactic acid bacteria isolated from corn stovers. Anim. Sci. J. 82, 642–653. doi: 10.1111/j.1740-0929.2011.00894.x

Ohno, H., Nishio, S., Tsurii, J., Kawamoto, T., Sonomoto, K., and Nakayama, J. (2014). Monitoring of the microbiota profile in nukadoko, a naturally fermented rice bran bed for pickling vegetables. J. Biosci. Bioeng. 118, 520–525. doi: 10.1016/j.jbiosc.2014.04.017

Osimani, A., Garofalo, C., Aquilanti, L., Milanovici, V., and Clementi, F. (2015). Unpasteurised commercial boza as a source of microbial diversity. Int. J. Food Microbiol. 194C, 62–70. doi: 10.1016/j.ijfoodmicro.2014.11.011

Ouoba, L. I., Lei, V., and Jensen, L. B. (2008). Resistance of potential probiotic lactic acid bacteria and bifidobacteria of African and European origin to antimicrobials, determination and transferability of the resistance genes to other bacteria. Int. J. Food. Microbiol. 121, 217–224. doi: 10.1016/j.ijfoodmicro.2007.11.018

Pepe, O., Villani, F., and Coppola, S. (2001). Differential viable count of mixed starter cultures of lactic acid bacteria in doghgs by using modified
Chalmers medium. Microbiol. Res. 155, 351–354. doi: 10.1016/S0944-5013(01)80015-X

Pereira, C. I., San Román, M. V., Lolkema, J. S., and BarretoCrespo, M. T. (2009). Weissella halotolerans W22 combines arginine deiminase and ornithinecarboxylation pathways and converts arginine to putrescine. J. Appl. Microbiol. 107, 1894–1902. doi: 10.1111/j.1365-2672.2009.04371.x

Ponnamusamy, K., Choi, J. N., Kim, J., Lee, S. Y., and Lee, C. H. (2011). Microbial community and metabolomic comparison of irritable bowel syndrome faeces. J. Med. Microbiol. 60, 817–827. doi: 10.1099/jmm.0.028126-0

Połtakos, V., Taminaia, B., Huys, G., Nezer, C., Daube, G., and Devlieghere, F. (2014). Psychrotrophic lactic acid bacteria associated with production batch recalls and sporadic cases of early spoilage in Belgium between 2010 and 2014. Int. J. Food Microbiol. 191, 157–163. doi: 10.1016/j.ijfoodmicro.2014.09.013

Pringsulaka, O., Patarsarinsilpboon, N., Suwannasai, N., Atthakor, W., and Rangsuri, A. (2011). Isolation and characterisation of a novel Pseudoliriodenephal infecting Weissella cibaria N 22 from Nham, a Thai fermented pork sausage. Food Microbiol. 28, 518–525. doi: 10.1016/j.fmid.2010.01.011

Rao, T. J., and Goyal, A. (2013a). Purification, optimization of assay, and stability studies of dextranase isolated from Weissella cibaria JAG8. Prep. Biochem. Biotechnol. 43, 329–341. doi: 10.1080/20260682.2012.737400

Rao, T. J., and Goyal, A. (2013b). A novel high dextran yielding lactic acid bacteria as probiotics for juvenile seabass. Int. J. Food Microbiol. 161, 79–89. doi: 10.1016/j.ijfoodmicro.2012.10.018

Sarmenta, C., Klotz, P., de Carvalho, A. J. C., Gomes, M., and Schillinger, U. (2013). Detection and quantification of Weissella cibaria sp. nov., isolated from plaa-som, a fermented fish product from Thailand. Int. J. Food Microbiol. 165, 157–163. doi: 10.1016/j.ijfoodmicro.2013.08.019

Scheirlinck, I., Van der Meulen, R., Van Schoor, A., Vancanneyt, M., De Vuyst, L., and Schillinger, U. (2014). “The genus Enterococcus,” in Handbook of New Bacterial Systematics, eds M. Goodfellow and A. G. O’Donnell (London: Academic Press Ltd), 151–194.

Sharma, M. C., Head, M. B., and Dicks, L. M. (2003). Identification of lactic acid bacteria isolated from plaa-som, a fermented fish product from Thailand. Int. J. Food Microbiol. 73, 224–230. doi: 10.1016/S0168-1605(99)00315-5

Scheirlinck, I., Van der Meulen, R., Van Schoor, A., Vancanneyt, M., De Vuyst, L., Pandemare, P., et al. (2007). Influence of geographical origin and flour type on diversity of lactic acid bacteria in traditional Belgian sourdoughs. Appl. Environ. Microbiol. 73, 6262–6269. doi: 10.1128/AEM.00894-07

Schillinger, U., Boehringer, L., Wallbaum, S., Caroline, L., Gona, A., Huch Née Koritnik, M., et al. (2008). A genus-specific PCR method for differentiation between Leuconostoc and Weissella and its application in identification of heterofermentative lactic acid bacteria from coffee fermentation. FEMS Microbiol. Lett. 286, 222–226. doi: 10.1111/j.1574-6968.2008.01286.x

Schwab, C., Mastrangelo, M., Corsetti, A., and Gänzle, M. (2008). Formation of oligosaccharides and polysaccharides by Lactobacillus reuteri LTH5448 and Weissella cibaria 10M in sorghum sourdoughs. Cereal Chem. 85, 679–684. doi: 10.1094/FCMHEM-85-5-0679

Sengun, I. Y., Nieben, D. S., Karapinar, M., and Jakobsen, M. (2009). Identification of lactic acid bacteria isolated from Tarhana, a traditional Turkish fermented food. Int. J. Food Microbiol. 135, 105–111. doi: 10.1016/j.ijfoodmicro.2009.07.033

Serna-Cock, L., Vallejo-Castillo, V. E., and Garcia-Gonzalez, E. (2013). Effects of wall materials and lyophilization on the viability of Weissella confusa. African J. Biotechnol. 13, 2661–2667. doi: 10.5897/AJB2013.13860

Shin, J. H., Kim, D. I., Kim, H. R., Kim, D. S., Kook, J. K., and Lee, J. N. (2007). Severe infective endocarditis of native valves caused by Weissella confusa detected incidentally on echocardiography. J. Infect. 54, 149–151. doi: 10.1016/j.jinf.2006.09.009

Shukla, S., Shi, Q., Maina, N. H., Juvenon, M., Majatkenan, and Goyal, A. (2014). Weissella confusa Cab3 dextranuse: properties and in vitro synthesis of dextran and glucoligosaccharides. Carbohydr. Polym. 101, 554–564. doi: 10.1016/j.carbpol.2013.09.087

Sica, M. G., Olivera, N. L., Brugnoni, L. L. Marucci, P. L., Lóz-Cazorla, A. C., and Cubitto, M. A. (2010). Isolation, identification and antimicrobial activity of lactic acid bacteria from the Bahia Blanca estuary. Rev. Biol. Mar. Oceanogr. 45, 389–397. doi: 10.4067/S0718-19572010000300006

Silverstein, M. E., and Hicks, D. M. (2003). Identification of lactic acid bacteria isolated from human vaginal secretions. Antonie van Leeuwenhoek 83, 117–123. doi: 10.1002/ajiv.20311

Sirirat, R., Thosaporn, R., and Somkiat, P. (2008). Evaluations of lactic acid bacterial as probiotics for juvenile seabass Lates calcarifer. Aquac. Res. 39, 134–143. doi: 10.1111/j.1365-2109.2007.01864.x

Sirirat, R., Thosaporn, R., and Somkiat, P. (2008). Evaluations of lactic acid bacterial as probiotics for juvenile seabass Lates calcarifer. Aquac. Res. 39, 134–143. doi: 10.1111/j.1365-2109.2007.01864.x

Skerman, V. B. D., McGowan, V., and Sneath, P. H. A. (eds.). (1989). Approved Lists of Bacterial Names, Amended Edition. Washington, DC: American Society for Microbiology.

Snooawart, I., Papalexandratou, Z., De Vuyt, L., and Vandamme, P. (2013). Characterization of strains of Weissella faibalis sp. nov. and Fructobacillus tractorpoli from spontaneous cocoa bean fermentations. Int. J. Syst. Evol. Microbiol. 63, 1709–1716. doi: 10.1099/ijs.0.03410-0

Snyder, A. K., Hinsaw, J. M., and Welch, T. J. (2014). Diagnostic tools for rapid detection and quantification of Weissella ceti NC63 infections in rainbow trout. Lett. Appl. Microbiol. 60, 103–110. doi: 10.1111/lam.12365

Srivastava, M. K., Sinha, S., and Shukla, A. K. (2012). “Weissella,” in The Probiotic Bacteria, ed. B. B. Singh (Boca Raton, FL: CRC Press), 551–563.

Srivastava, M. K., Sinha, S., and Shukla, A. K. (2012). “Weissella,” in The Probiotic Bacteria, ed. B. B. Singh (Boca Raton, FL: CRC Press), 551–563.

Srivastava, M. K., Sinha, S., and Shukla, A. K. (2012). “Weissella,” in The Probiotic Bacteria, ed. B. B. Singh (Boca Raton, FL: CRC Press), 551–563.

Srivastava, M. K., Sinha, S., and Shukla, A. K. (2012). “Weissella,” in The Probiotic Bacteria, ed. B. B. Singh (Boca Raton, FL: CRC Press), 551–563.

Srivastava, M. K., Sinha, S., and Shukla, A. K. (2012). “Weissella,” in The Probiotic Bacteria, ed. B. B. Singh (Boca Raton, FL: CRC Press), 551–563.

Srivastava, M. K., Sinha, S., and Shukla, A. K. (2012). “Weissella,” in The Probiotic Bacteria, ed. B. B. Singh (Boca Raton, FL: CRC Press), 551–563.
fermented fish in Thailand. Int. J. Syst. Evol. Microbiol. 50, 1479–1485. doi: 10.1099/0027713-30-4-1479

Tanasupawat, S. I., Okada, S., and Komagata, K. (1998). Lactic acid bacteria found in fermented fish in Thailand. J. Gen. Appl. Microbiol. 44, 193–200. doi: 10.2323/jam.44.193

Thongsansit, I., Tanikawa, M., Yano, S., Tpachiki, T., and Wakayam, M. (2009). Identification of glutaminase-producing lactic acid bacteria isolated from Nham, a traditional Thai fermented food and characterisation of glutaminase activity of isolated Weissella cibaria. Ann. Microbiol. 59, 715–720. doi: 10.1007/BF03179213

Tiekink, M., Korakli, M., Ehrmann, M. A., Ganzle, M. G., and Vogel, R. F. (2003). In situ production of exopolysaccharides during sourdough fermentation by cereal and intestinal isolates of lactic acid bacteria. Appl. Environ. Microbiol. 69, 945–952. doi: 10.1128/AEM.69.2.945-952.2003

Tsakalidou, E., Samelis, J., Metaxopoulos, J., and Kalantzopoulos, G. (1997). Atypical Leuconostoc-like Weissella strains isolated from meat, sharing low phenotypic relatedness with the so far recognized arginine-negative Weissella spp. revealed by SDS-PAGE of whole cell proteins. Syst. Appl. Microbiol. 20, 659–664. doi: 10.1016/S0723-2020(97)80039-2

Urso, R., Comi, G., and Cocolin, L. (2006). Ecology of lactic acid bacteria in Italian fermented sausages: isolation, identification and molecular characterization. Syst. Appl. Microbiol. 29, 671–680. doi: 10.1016/j.syapm.2006.01.012

Vahjen, W., Pieper, R., and Zentek, J. (2010). Bar-coded pyrosequencing of 16S rDNA gene amplicons reveals changes in ileal porcine bacterial communities due to high dietary zinc intake. Appl. Environ. Microbiol. 76, 6689–6691. doi: 10.1128/AEM.03075-09

Vela, A. I., Fernández, A., de Quirós, Y. B., Herráez, P., Domínguez, L., and Vela, A. I., Porren, G., Goyache, J., Nieto, A., Sánchez, B., Briones, V., et al. (2003). Weissella confusa infection in primate (Cercopithecus mona). Emerg. Infect. Dis. 9, 1307–1309. doi: 10.3201/eid9010.020667

Vitali, B., Minervini, G., Rizzello, C. G., Spini, E., Maccasferri, S., Brigidi, P., et al. (2012). Novel probiotic candidates for humans isolated from raw fruits and vegetables. Food Microbiol. 31, 116–125. doi: 10.1016/j.fm.2011.12.027

Walker, J., Hertel, C., Tannock, G. W., Lis, C. M., Munro, K., and Hammes, W. P. (2001). Detection of Lactobacillus, Pediococcus, Leuconostoc, and Weissella species in human feces by using group-specific PCR primers and denaturing gradient gel electrophoresis. Appl. Environ. Microbiol. 67, 2578–2585. doi: 10.1128/AEM.67.6.2578-2585.2001

Wang, C., Zhang, C. W., Chen, H. C., Yu, Q., Pei, X. F., and Liu, H. C. (2008). Phylogenetic analysis and identification of two bacterial strains sourcing from human intestine and having resistance to acid and bile. Sichuan Da Xue Xue Bao Yi Xue Ban 39, 263–268.

Wang, J. P., Yoo, J. S., Jang, H. D., Lee, J. H., Cho, J. H., and Kim, I. H. (2011). Effect of dietary fermented garlic by Weissella koreensis powder on growth performance, body characteristics, and immune response of growing pigs challenged with Escherichia coli lipopolysaccharide. J. Anim. Sci. 89, 2123–2131. doi: 10.2527/jas.2010-3186

Welch, T. J., and Good, C. M. (2013). Mortality associated with Weissellosis (Weissella sp.) in USA farmed rainbow trout: potential for control by vaccination. Aquaculture 388–391, 122–127. doi: 10.1016/j.aquaculture.2013.01.021

Welch, T. J., Marancik, D. P., and Good, C. M. (2014). “Weissellosis,” in AFS-FHS (American Fisheries Society-Fish Health Section). FHS Blue Book: Suggested Procedures for the Detection and Identification of Certain Fish and Shellfish Pathogens, 2014 edition. 1.3.4, 1–10. Available online at: http://afs-fhs.org/bluebook/bluebook-index.php

Wolter, A., Hager, A. S., Zannini, E., Czerny, M., and Arendt, E. K. (2014). Influence of dextran-producing Weissella cibaria on baking properties and sensory profile of gluten-free and wheat breads. Int. J. Food Microbiol. 172, 83–91. doi: 10.1016/j.ijfoodmicro.2013.11.015

Wouters, D., Grosu-Tudor, S., Zamfir, M., and De Vuyst, L. (2013). Bacterial community dynamics, lactic acid bacteria species diversity and metabolite kinetics of traditional Romanian vegetable fermentations. J. Sci. Food Agric. 93, 749–760. doi: 10.1002/jsfa.5788

Wu, R., Wang, L., Wang, J., Li, H., Menghe, B., Wu, J., et al. (2009). Isolation and preliminary probiotic selection of lactobacilli from koumiss in inner Mongolia. J. Basic Microbiol. 49, 318–326. doi: 10.1002/jobm.200800047

Yangida, F., Chen, Y. S., and Yasaki, M. (2007). Isolation and characterization of lactic acid bacteria from lakes. J. Basic Microbiol. 47, 184–190. doi: 10.1002/jobm.200610237

Yang, J., Ji, Y., Park, H., Lee, J., Park, S., Yoo, S., et al. (2014). Selection of functional lactic acid bacteria as starter cultures for the fermentation of Korean leek (Allium tuberosum Rottler ex Sprengel). Int. J. Food Microbiol. 191C, 164–171. doi: 10.1016/j.ijfoodmicro.2014.09.016

Yoshiyama, M., Wu, M., Sugimura, Y., Takaya, N., Kimoto-Nira, H., and Suzuki, C. J. (2013). Inhibition of Paenibacillus larvae by lactic acid bacteria isolated from fermented materials. Invertebr. Pathol. 112, 62–67. doi: 10.1016/j.ijip.2012.09.002

Zambou, N. F., Sieladie, D. V., Fonteh, F. A., Moundipa, P. F., Tchouanguep, F. M., and El Soda, M. (2008). Phenotypic characteristics of lactic acid bacteria isolated from cow’s raw milk of Bororo cattle breeders in Western Highland Region of Cameroon. Res. J. Microbiol. 3, 447–456. doi: 10.1093/rjm/2008.447.456

Zamudio-Maya, M., Narváez-Zapata, J., and Rojas-Herrera, R. (2008). Isolation and identification of lactic acid bacteria from sediments of a coastal marsh using a differential selective medium. Lett. Appl. Microbiol. 46, 402–407. doi: 10.1111/j.1472-765X.2008.02329.x

Zannini, E., Mauch, A., Galle, S., Gänzle, M., Coffey, A., Arendt, E. K., et al. (2013). Barley malt wort fermentation by exopolysaccharide-forming Weissella cibaria MG1 for the production of a novel beverage. J. Appl. Microbiol. 115, 1357–1387. doi: 10.1111/jam.12329

Zhang, Z., Peng, X., Zhang, N., Liu, L., Wang, Y., and Ou, S. (2014). Cytotoxicity comparison of quercetin and its metabolites from in vitro fermentation of several gut bacteria. Food Funct. 5, 2152–2156. doi: 10.1039/C4FO00418C

Zhao, Z. G., Quan, W. R., Li, G. H., An, C. M., and Cui, Y. X. (2008). The isolated lipopolysaccharide from Mesoplodon bidens found in fermented fish in Thailand. Int. J. Syst. Evol. Microbiol. 63, 1417–1420. doi: 10.1099/ijs.0.043612-0

Zhang, Z., Cui, Y., Li, G., Liu, L., and Ou, S. (2013). Novel probiotic candidates for humans isolated from raw fruits and vegetables. Food Sci Technol. 5, 11–13.

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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