18 The Family *Leuconostocaceae*

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Abstract
Leuconostocaceae are lactic acid bacteria (LAB) belonging to order *Lactobacillales*. The family consists of genera *Leuconostoc*, *Weissella*, *Oenococcus*, and *Fructobacillus*. The genus *Leuconostoc* was described already in 1878 by van Tieghem. The oldest described species belonging to *Oenococcus* and *Fructobacillus* were originally described as *Leuconostoc* spp. but were later reclassified based on phenotypic and phylogenetic studies. Genus *Weissella* contains species originally classified as *Leuconostoc* or *Lactobacillus* spp.

Like other LAB, *Leuconostocaceae* are Gram positive, catalase negative, and chemoorganotrophic. They grow in rich media supplemented with growth factors and amino acids and generate energy by substrate-level phosphorylation. *Leuconostocaceae* ferment glucose heterofermentatively yielding lactic acid, CO_2, ethanol, and/or acetate.

Leuconostocaceae are found in environments with high nutrient content, e.g., on green vegetation, roots, and food. Within LAB, *Leuconostocaceae* are characterized by their adaptable fermentation patterns that enable efficient generation of ATP from carbohydrates and, consequently, enhanced growth. Due to their ability to grow rapidly in rich media under elevated CO_2 concentration at moderate temperatures, *Leuconostocaceae* are competitive in various food environments and contribute to a number of fermentation processes. The diverse fermentation substrates and products of *Leuconostocaceae* may cause desired or undesired effects on the organoleptic quality of foods.

This contribution is a modified and updated version of previous descriptions of the family (Schleifer, 2009) and the included genera (Björkroth et al., 2009; Björkroth and Holzapfel, 2006; Dicks and Holzapfel, 2009; Holzapfel et al., 2009).

Taxonomy, Historical and Current

The family *Leuconostocaceae* belongs to the order *Lactobacillales*. Since the late 2000s, this family has contained the genera of *Fructobacillus*, *Leuconostoc*, *Oenococcus*, and *Weissella*. The genus *Leuconostoc* has been the hub of taxonomic reclassifications leading to description of the three other genera.

Historically, *Leuconostoc mesenteroides* was first mentioned by Van Tieghem in 1878 (Van Tieghem 1878) in an article called "Sur la Gomme de Sucrerie (*Leuconostoc mesenteroides*)." The description of the genus *Leuconostoc* is following today the lines published by Garvie (1986). The taxonomic revisions affecting leuconostocs have mainly been due to implementation of phylogenetic analyses and the studies utilizing polyphasic taxonomy approaches. The first phylogenetic analyses of the 16S rRNA gene sequences (Martinez-Murcia and Collins 1990; Martinez-Murcia et al. 1993) resulted in recognition of three distinct lineages within leuconostocs. They were referred as the genus

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Leuconostoc sensu stricto, the *Leuconostoc paramesenteroides* group, and *Leuconostoc oenos*. A new genus *Weissella* (Collins et al. 1993) was described to accommodate members of the so-called *L. paramesenteroides* group (including *L. paramesenteroides* and some atypical, heterofermentative lactobacilli). In addition, *L. oenos* has been reclassified as *Oenococcus oeni* (Dicks et al. 1995). More recently, some atypical leuconostocs of plant origin including *Leuconostoc durionis*, *Leuconostoc ficulneum*, *Leuconostoc fructosum*, and *Leuconostoc pseudoficulneum* have been assigned to the new genus *Fructobacillus* (Endo and Okada 2008). After these reclassifications, the genus *Leuconostoc* includes 13 validly published species names (*Table 18.1*) with *L. mesenteroides* as the type species. *L. mesenteroides* is the only species divided into subspecies which have not been established based on phylogenetic or genomic boarders. According to Vancanneyt et al. (2006), *Leuconostoc argentinum* (Dicks et al. 1993) is a later synonym of *Leuconostoc lactis*.

With the exception of *Leuconostoc fallax*, 16S rRNA gene sequence similarities among the type strains of *Leuconostoc* spp. are high, varying from 97.3 % to 99.5 % (Björkroth and Holzapfel 2006). 16S rRNA gene sequence analysis further divides leuconostocs into three evolutionary branches including *Leuconostoc citreum*, *Leuconostoc holzapfelii*, *Leuconostoc lactis*, and *Leuconostoc palmae* in the first branch; *L. mesenteroides* and *L. pseudomesenteroides* in the second; and *Leuconostoc carnosum*, *Leuconostoc gasicomitatum*, *Leuconostoc gelidum*, *Leuconostoc inhae*, and *Leuconostoc kimchii* in the third branch, whereas *L. fallax* is genetically more distinct from the other *Leuconostoc* species (*Fig. 18.1*).

In addition to the 16S rRNA gene, the loci of housekeeping genes *atpA*, *dnaK*, *pheS*, *recN*, and *rpoA* in leuconostocs have been analyzed. The phylogenetic trees constructed on analyses of *pheS*, *rpoA*, and *atpA* loci offered discriminatory power for differentiation of species within the genus *Leuconostoc* and were roughly in agreement with 16S rRNA gene-based phylogeny (Ehrmann et al. 2009; De Bruyne et al. 2007). Comparative sequencing of the additional phylogenetic markers *dnaK* and *recA* confirmed the 16S rRNA gene tree topology in the study describing *L. palmae* (Ehrmann et al. 2009). Arahal et al. (2008) studied the usefulness of *recN* locus and concluded that also *recN* can serve as a phylogenetic marker as well as a tool for species identification. Congruence of evolutionary analyses inside the *Leuconostoc–Oenococcus–Weissella* clade has been assessed by comparative phylogenetic analyses of 16S rRNA, *dnaA*, *gyrB*, *rpoC*, and *dnaK* housekeeping genes (Chelo et al. 2007). Phylogenies obtained with the different genes were in overall good agreement, and a well-supported almost fully resolved phylogenetic tree was obtained when the combined sequence data were analyzed using a Bayesian approach.

Within the genus *Weissella*, several new species have been characterized during the last 5 years, and the genus currently comprises 17 species (*Table 18.2*). The description for the genus is as published by Collins et al. (1993). The type species is *Weissella viridescens* (Niven and Evans 1957) which is synonymous to *Lactobacillus viridescens*.

The genus *Weissella* was proposed by Collins et al. (1993), and the first species included in this genus comprises species previously classified as *Leuconostoc* or *Lactobacillus*. *L. paramesenteroides* (Garvie 1967a), *L. viridescens* (Niven and Evans 1957; Kandler and Abo-Elnaga 1966), *Lactobacillus confusus* (Holzapfel and Van Wyk 1982; Holzapfel and Kandler 1969), *Lactobacillus kandleri* (Holzapfel and Van Wyk 1982), *Lactobacillus minor* (Kandler et al. 1983), and *Lactobacillus halotolerans* (Kandler et al. 1983) kept their specific epithets and were reclassified as *Weissella paramesenteroides*, *W. viridescens*, *Weissella confusa*, *W. kandleri*, *Weissella minor*, and *Weissella halotolerans*, respectively. These species were followed by inclusion of *Weissella hellenica* (Collins et al. 1993), *Weissella thailandensis* (Tanasupawat et al. 2000), *Weissella cibaria* (Björkroth et al. 2002), *Weissella soli* (Magnusson et al. 2002), and *Weissella koreensis* (Lee et al. 2002). In addition, *Weissella kimchii* was proposed by Choi et al. (2002), but it was found as a later heterotypic synonym of *Weissella cibaria* (Ennahar and Cai 2004). *Weissella ghanensis* (De Bruyne et al. 2008), *Weissella beninensis* (Padonou et al. 2010) and *Weissella fabaria* (De Bruyne et al. 2010), *Weissella ceti* (Vela et al. 2011), *Weissella fabalis* (Snauwaert et al. 2013), and *Weissella oryzae* (Tohno et al. 2012) are the latest species suggested to the genus *Weissella*.

W. confusa, *W. cibaria*, *W. halotolerans*, *W. hellenica*, *W. kandleri*, *W. koreensis*, *W. minor*, *W. paramesenteroides*, *W. soli*, *W. thailandensis*, and *W. viridescens* share 93.9–99.2 % 16S rRNA encoding gene sequence similarity (Björkroth et al. 2009). Among the recently described species, sequence similarity analyses (Snauwaert et al. 2013) indicated that *W. fabalis* type strain shares the highest sequence similarities with the type strains of *W. fabaria* (97.7 %), *W. ghanensis* (93.3 %), and *W. beninensis* (93.4 %). Five main phylogenetic branches exist based on the 16S rRNA encoding gene analyses. *W. hellenica*, *W. paramesenteroides*, and *W. thailandensis* branch together, as do *W. cibaria* and *W. confusa*. Two other branches are formed by *W. ceti*, *W. minor*, *W. halotolerans*, and *W. viridescens* in one branch and *W. kandleri*, *W. koreensis*, *W. oryzae*, and *W. soli* in another. *W. fabali* s (Snauwaert et al. 2013), *W. fabaria* (De Bruyne et al. 2010), and *W. ghanensis* (De Bruyne et al. 2008) form the fifth branch distinct from the other species within the genus.

Oenococcus oeni, type species of the genus *Oenococcus*, had been formerly classified as *Leuconostoc oenos* (Garvie 1967b). The genus *Oenococcus* currently includes two species, which are *Oenococcus kitaharae* and *O. oeni*. *O. oeni* was formerly classified as *Leuconostoc oenos* and reclassified as a member of the novel genus *Oenococcus* (Dicks et al. 1995). A candidate of novel *Oenococcus* species might have been isolated from bioethanol fermenting tank (Lucena et al. 2010), which has not been characterized at a time of writing (September, 2012). Originally, the species *O. oeni* was considered as a genetically homogeneous organism based on the sequencing of rRNA operon (Jeune and Lonvaud-Funel 1997; Zavaleta et al. 1996). However, recent study by Bridier et al. (2010) found diverse genetic groups in the species by multilocus sequence typing (MLST) with sequences

Table 18.1

Phenotypic characteristics of *Leuconostoc* spp.

Characteristics	*L. mesenteroides* ssp.				*L. lactis*	*L. pseudomesenteroides*	*L. citreum*	*L. carnosum*	*L. gelidum*	*L. fallax*	*L. kimchii*	*L. gasicomitatum*	*L. inhae*	*L. holzapfelii*	*L. palmae*	*L. miyukkimchii*
	mesenteroides	*dextranicm*	*cremoris*	*suionicum*												
Acid from																
Amygdalin	d	ND	–	+	–	d	d	–	+	ND	+	–	d	–	ND	+
L-Arabinose	+	–	–	+	d	d	+	–	+	–	–	+	+	+	–	–
Arbutin	d	–[a]	–	+	–	d	+	–	+	–	ND	–	–	–	ND	+
Cellobiose	d	d	–	+	–	d	+	d	+	–	+	+	+	–	–	+
Galactose	+	d	+	+	+	d	d	–	–	–	+	d	d	+	ND	–
Lactose	d	d	d		+	d	–	–	–	–	+	–	–	–	ND	–
Maltose	+	+	–	+	+	+	+	–	d	+	+	+	+	+	–	+
Mannitol	d	(d)	–	d	–	–	d	–	–	(d)	+	–	+	–	–	+
Mannose	d	d[a]	–	+	+	+	+	d	+	+	+	+	+	+		+
Melibiose	d	d	–	+	d	d	–	d	+	–	ND	+	–	+	–	–
Raffinose	d	d[a]	–	–	d	d	–	–	+	–	–	+	–	+	–	–
Ribose	d	+[a]	–	+	–	+	–	d	d	+	+	+	+	–		+
Salicin	d	d	–	+	d	d	+	d	+	–	+	–	d	–	–	+
Starch	–	–[a]		–	–	d	–	ND	ND	ND	–	–	–	–	ND	+
Sucrose	+	+	–	+	+	d	+	+	+	+	+	+	+	–	+	+
Trehalose	+	+	–	+	d	+	+	+	+	(d)	+	+	+	+	–	+
D-Xylose	d	d	–	+	–	+	d	–	+	–	–	–	–	–	ND	+
Hydrolysis of aesculin	+	d	–	+	–	d	+	d	+	ND	ND	+	+	–	ND	+
Dextran production	+[a]	+[a]	–[a]	ND	–[a]	ND	ND	d[b]	d	ND	+[a]	+	ND	+	ND	ND
Growth at pH 4.8	–[a]	–[a]	–[a]	ND	–[a]	ND	ND	ND	ND	ND	ND	ND	+	+	ND	–
Growth at 37 °C	d[a]	+	–[a]	+	+[a]	+	d	–	–	+	+	–	–	+	ND	–
Peptidoglycan type	Lys-Ser-Ala_2[a]	Lys-Ser-Ala_2[a]	Lys-Ser-Ala_2[a]	ND	Lys-Ala_2[a]	Lys-Ser-Ala_2[a]	Lys-Ala_2[a]	Lys-Ala_2[a]	Lys-Ala_2[a]	Lys-Ala_2	ND	Lys-Ala_2	ND	ND	ND	ND
References and the number of strains examined	Farrow et al. (1989) ($n = 30$)	Garvie (1976) ($n = 21$)	Farrow et al. 1989 ($n = 14$)	Gu et al. (2012) ($n = 2$)	Farrow et al. (1989) ($n = 4$)	Farrow et al. (1989) ($n = 7$)	Farrow et al. (1989) ($n = 11$)	Shaw and Harding (1989) ($n = 15$)	Shaw and Harding (1989) ($n = 30$)	Holzapfel et al. (2009)	Kim et al. (2000a) ($n = 1$)	Björkroth et al. (2000) ($n = 4$)	Kim et al. (2003) ($n = 6$)	De Bruyne et al. (2007) ($n = 1$)	Ehrmann et al. (2009) ($n = 1$)	Lee et al. (2012b) ($n = 1$)

+, 90 % or more of strains positive; –, 90 % or more of strains negative; d, 11–98 % of strains positive; (), delayed reaction

ND no data

[a]Holzapfel et al. (2009)

[b]Björkroth et al. (1998)

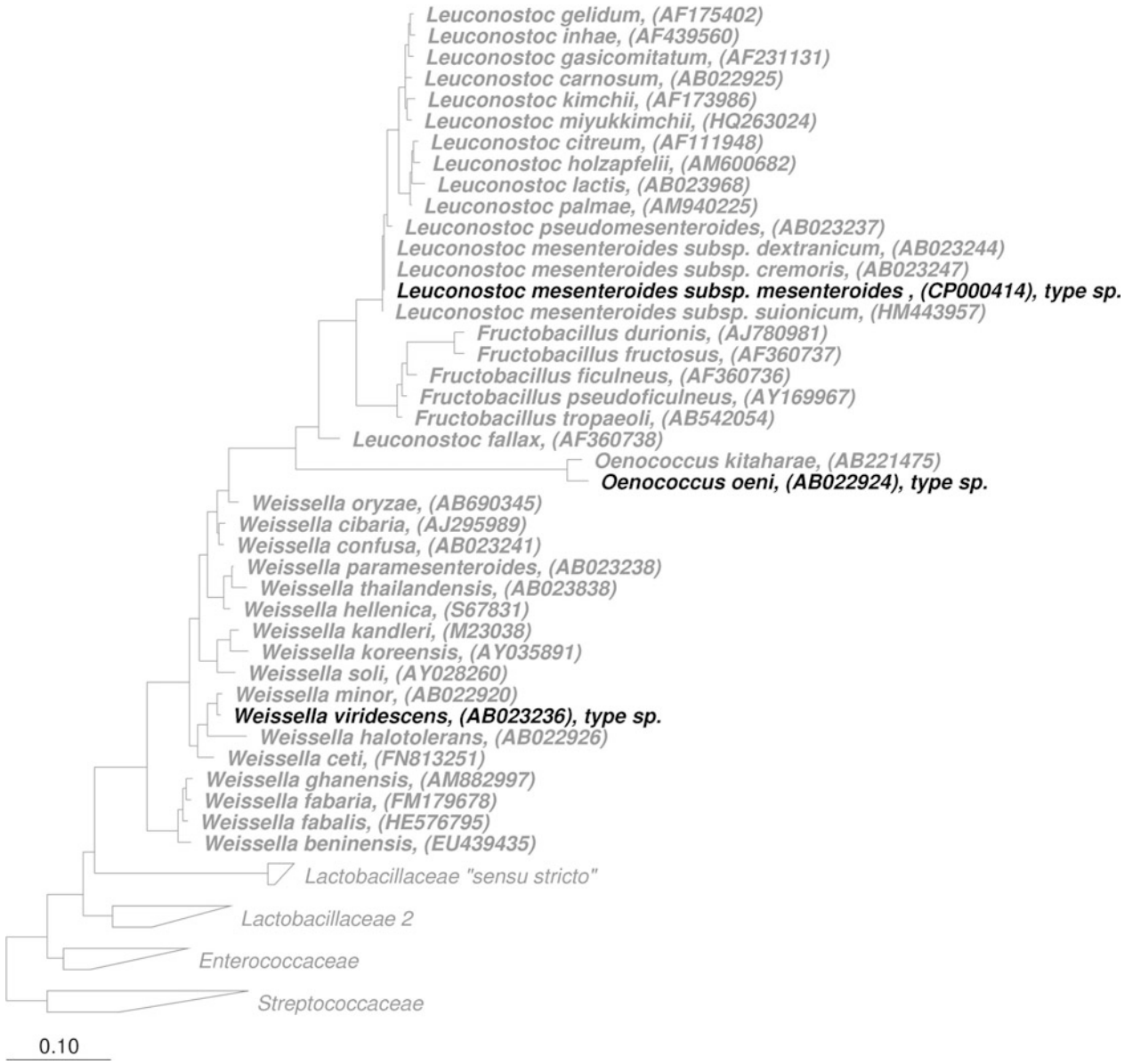

Fig. 18.1

Phylogenetic reconstruction of the family *Leuconostocaceae* based on 16S rRNA and created using the maximum likelihood algorithm RAxML (Stamatakis 2006).The sequence datasets and alignments were used according to the All-Species Living Tree Project (LTP) database (Yarza et al. 2010; http://www.arb-silva.de/projects/living-tree). Representative sequences from closely related taxa were used as outgroups. In addition, a 40 % maximum frequency filter was applied in order to remove hypervariable positions and potentially misplaced bases from the alignment. Scale bar indicates estimated sequence divergence

of several housekeeping genes. Reclassification of *L. oenos* into the genus *Oenococcus* was carried out based on its unique phylogenetic position, physiological characteristics, total soluble cell protein analysis, and several biochemical characteristics by Dicks et al. (1995). Already in 1993 Martinez-Murcia et al. (1993) showed by comparison of both 16S and 23SrRNA sequences that *L. oenos* does not belong to the same line of descent with the *L. sensu stricto* organisms or *L. paramesenteroides* group of species (the current genus *Weissella*). The second species, *O. kitaharae*, was described from compost of distilled *shochu* residue in Japan (Endo and Okada 2006). These two species share 96.0 % similarity based on 16S rRNA gene sequence. Sequence similarities with other members of family *Leuconostocaceae* are less than 85 %. The high level of phylogenetic divergence of the genus *Oenococcus* compared to that of the other lactic acid bacteria might be explained by the absence of the mismatch mutation repair system in oenococci, which causes a high mutation rate, an excess of recombination, and a rapid genetic evolution (Marcobal et al. 2008). Based on *pheS* sequences, *Oenococcus* spp. still belong to the family

Table 18.2
Phenotypic characteristics of *Weissella* spp.

Characteristics	*W. viridescens*	*W. paramesenteroides*	*W. confusa*	*W. halotolerans*	*W. kandleri*	*W. minor*	*W. hellenica*	*W. thailandensis*	*W. cibaria*	*W. koreeensis*	*W. soli*	*W. ghanensis*	*W. beniensis*	*W. fabaria*	*W. ceti*	*W. fabalis*	*W. oryzae*
Acid from																	
Amygdalin	ND	ND	ND	ND	ND	ND	ND	–	+		–	+	+	–	–	–	–
L-Arabinose	–	d	–	–	–	–	+	+	+	+	+	–	+	–	–	–	+
Arbutin	ND	ND	ND	ND	ND	ND	ND	ND	+	ND	–	+	+	–	–	–	–
Cellobiose	–	(d)	+	–	–	+	–	–	+	–	–	+	d	+	–	+	–
Fructose	ND	ND	ND	ND	ND	ND	ND	+	+	ND	–	+	+	+	–	+	+
Galactose	–	+	+	–	+	–	–	+	–	–	–	–	+	–	–	–	(+)
Lactose	ND	ND	ND	ND	ND	ND	ND	–	–	ND	–	–	+	–	–	–	–
Maltose	+	+	+	+	–	+	+	+	+	–	+	+	+	–	+	+	+
Mannitol	ND	ND	ND	ND	ND	ND	ND	–	–	ND	–	–	+	+	–	–	–
Mannose	ND	ND	ND	ND	ND	ND	ND	+	+	ND	+	+	+	+	–	+	+
Melibiose	–	+	–	–	–	–	–	+	–	–	+	–	+	–	–	–	(+)
Raffinose	–	d	–	–	–	–	–	+	–	–	+	–	+	–	–	–	–
Ribose	–	ND	+	+	+	+	–	+	–	+	+	–	d	–	+	–	+
Salicin	ND	ND	ND	ND	ND	ND	ND	–	+	ND	+	+	d	–	–	–	–
Sucrose	d	+	+	–	–	+	+	+	+	–	+	d	+	–	–	–	–
Trehalose	d	+	–	–	–	+	+	+	–	–	+	+	d	+	+	+	+
D- Xylose	–	d	+	–	–	–	–	–	+	+	+	–	–	–	–	–	+
Ammonia from arginine	–	–	+	+	+	+	–	–	+	+	+	+	+	+	d	+	+
Hydrolysis of aesculin	–	ND	+	–	–	+	ND	–	+	–	ND	+	+	+	+	+	–
Gas from glucose	ND	ND	ND	ND	ND	ND	ND	+	+	+	ND	d	+	+	–	+	+
Lactic acid configuration	DL	D	DL	DL	DL	DL	D	D	DL	D	D	D or DL	DL	DL	DL	D	D

Table 18.2 (continued)

Characteristics	*W. viridescens*	*W. paramesenteroides*	*W. confusa*	*W. halotolerans*	*W. kandleri*	*W. minor*	*W. hellenica*	*W. thailandensis*	*W. cibaria*	*W. koreeensis*	*W. soli*	*W. ghanensis*	*W. beniensis*	*W. fabaria*	*W. ceti*	*W. fabalis*	*W. oryzae*
Dextran production	ND	−	+	ND	+	−	−	−	+	+	−	+	d	+	−	+	−
Growth at 37°C	ND	ND	ND	ND	ND	ND	ND	+	+	+	+	+	ND	+	+	+	+
Peptidoglycan type	Lys-Ala-Ser	Lys-Ala_2 or Lys-Ser-Ala_2	Lys-Ala	Lys-Ala-Ser	Lys-Ala-Gly-Ala_2	Lys-Ser-Ala_2	Lys-Ala-Ser	Lys-Ala_2	Lys-Ala (Ser)-Ala	Lys-Ala-Ser	ND	ND	ND	Lys-Ala-Ser	ND	Lys-Ala-Ser	ND
Cell morphology	Short rods	Spherical or lenticular	Short rods thickened at one end	Irregular short or coccoid rods	Irregular rods	Irregular short or coccoid rods	Large spherical or lenticular cells	Coccoid	Short rods	Short rods or coccoid	Short rods	Short rods	Short rods or coccoid	Coccoid	Short rods or coccoid	Coccoid	Short rods or coccoid
References and the number of strains examined	Collins et al. (1993)	Collins et al. (1993)	Collins et al. (1993)	Collins et al. (1993)	Collins et al. (1993)	Collins et al. (1993)	Collins et al. (1993)	Tanasupawat et al. (2000) ($n = 5$)	Björkroth et al. (2002) ($n = 18$)	Lee et al. (2002) ($n = 2$)	Magnusson et al. (2002) ($n = 4$)	De Bruyne et al. (2008) ($n = 2$)	Padonou et al. (2010) ($n = 4$)	De Bruyne et al. (2010) ($n = 2$)	Vela et al. (2011) ($n = 9$)	Snauwaert et al. (2013) ($n = 1$	Tohno et al. (2012) ($n = 2$)

+, 90 % or more of strains positive; −, 90 % or more of strains negative; d, 11–98 % of strains positive; (), delayed reaction

ND no data

D, 90 % or more of the lactic acid is D(−), DL more than 25 % of the total lactic acid is L(+)

Leuconostocaceae but share different relationships with the other genera when compared to 16S rRNA gene sequence analyses. Sequence similarity of partial *pheS* gene between the two *Oenococcus* spp. is approximately 75 % and less than 70 % between *Oenococcus* spp. and other members in the family *Leuconostocaceae*. Related to the phylogeny, an interesting debate over its evolution speed has occurred. Because of a long branch in the 16S rRNA phylogenetic tree, *O. oeni* is regarded as "rapidly evolving" species (Yang and Woese 1989). This hypothesis was at first questioned based on data generated by *rpoB* gene sequences (Morse et al. 1996), but supported by comparative genome analyses of different species of lactic acid bacteria (LAB), including *O. oeni* (Makarova et al. 2006).

In addition to the 16S rRNA gene phylogeny, analysis with *pheS* (De Bruyne et al. 2010) and *recN* (Arahal et al. 2008) loci has been done. Congruence of evolutionary relationships inside the *Leuconostoc–Oenococcus–Weissella* clade has been assessed by phylogenetic analyses of 16SrRNA, *dnaA*, *gyrB*, *rpoC*, and *dnaK* (Chelo et al. 2007) housekeeping genes. Phylogenies obtained with the different genes were in overall good agreement, and a well-supported, almost fully resolved phylogenetic tree was obtained when the combined data were analyzed in a Bayesian approach.

The genus *Fructobacillus* currently includes five species. They are *F. durionis* (Leisner et al. 2005), *F. ficulneus* (Antunes et al. 2002), *F. fructosus* (Kodama 1956), *F. pseudoficulneus* (Chambel et al. 2006), and *F. tropaeoli* (Endo et al. 2011). With the exception of *F. tropaeoli*, these species were formerly classified as *Leuconostoc* species (Endo and Okada 2008). *Fructobacillus fructosus*, type species of the genus *Fructobacillus*, had been firstly classified as *Lactobacillus fructosus* based on morphological and physiological characteristics and later reclassified to *Leuconostoc fructosum* based on its phylogenetic position (Kodama 1956; Antunes et al. 2002). *Leuconostoc fructosum* was re-reclassified to *F. fructosus* based on physiological and morphological characteristics and its phylogenetic position (Endo and Okada 2008). Based on the 16S rRNA gene sequences, *Fructobacillus* species are phylogenetically separated into two subclusters. The first subcluster contains *F. fructosus* and *F. durionis* (97.9 % sequence similarity), and the second contains *Fructobacillus ficulneus*, *F. pseudoficulneus*, and *F. tropaeoli* (98.0–99.2 % sequence similarities). The sequence similarity between the two groups ranges from 94.2 % to 99.4 %. *Fructobacillus* species has been also genetically characterized based on sequences of 16S–23S rRNA gene intergenic spacer regions (ISR), *rpoC* and *recA*. Phylogenetic analysis based on the ISR and *rpoC* gene shows similar clustering to that based on 16S rRNA gene, but phylogenetic analysis based on *recA* gene shows different clustering (Endo and Okada 2008; Endo et al. 2011).

Molecular Analyses

Classification of the members of the family *Leuconostocaceae* using adequate molecular methods gives faster and more consistent and reliable results than schemes based on phenotypic characters. The molecular analyses have provided deeper insights into the phylogeny of the already assigned taxons within *Leuconostocaceae* and led to reclassification of species. In addition to the taxonomy and phylogeny, the motivation of many molecular studies has been more practical: to distinguish and identify relevant strains among closely related isolates. For the molecular characterization of *Leuconostocaceae*, various methods with differing resolving capacity have been reported and proposed; some have proven applicable for species identification, while others provide high discriminatory power and detail strain characterization. The choice of method depends on the scope and purpose of the study as well as on the availability of laboratory facilities. A summary of common molecular methods and their relative performances in differentiation of *Leuconostocaceae* is discussed below. In many studies cited, the results of two or more molecular methods have been combined to achieve better discrimination and more accurate clustering of the given set of isolates. However, only few studies report systematic comparison of different molecular methods and discuss their limitations for characterizing *Leuconostocaceae*.

DNA–DNA Hybridization Studies

DNA–DNA hybridization assays have been included in many studies to determine interspecies relationships among *Leuconostoc* and *Weissella* species and to reveal whether two isolates should be classified in the same species. Since many closely related species of *Fructobacillus*, *Leuconostoc*, or *Weissella* share high 16S rRNA gene sequence similarity, DNA–DNA hybridization experiments have been necessary to support a proposal for a novel species status.

DNA Fingerprinting

DNA fingerprinting using pulsed field gel electrophoresis (PFGE) and an appropriate restriction endonuclease provides high level of discrimination, allowing differentiation of closely related strains that are indistinguishable by other methods. Several investigators have used PFGE typing for characterizing *Leuconostocaceae* from dairy, meat, vegetable, and wine-related sources. These studies have demonstrated the success of PFGE typing in differentiating strains in a specific ecosystem or monitoring the presence of particular strains in a mixed population. For instance, PFGE typing has been used in several studies to study strain heterogeneity of *O. oeni* population during malolactic fermentation of wine (Sato et al. 2001; Vigentini et al. 2009; Zapparoli et al. 2012) as well as during an in-plant investigation of a ham spoilage problem to pinpoint potential sources of harmful *L. carnosum* contamination (Björkroth et al. 1998).

Another commonly used DNA fingerprinting technique is ribotyping or restriction fragment length polymorphism (RFLP) analysis of 16S and 23S rRNA genes where the detection of

ribotyping fingerprint is accomplished by hybridization with probes. Numerical analysis of ribotyping has been included in polyphasic taxonomy studies on *Leuconostoc* (Björkroth et al. 2000), *Fructobacillus* (Chambel et al. 2006) and *Weissella* (Björkroth et al. 2002) and found to provide species level identification with some intraspecies variation. Subsequently, ribotyping has been applied to detect and identify individual species or strains of *Leuconostocaceae* from various food, animal, and environmental sources. Although ribotyping provides discriminatory capacity for species identification, PFGE appears to be superior for strain differentiation (Björkroth et al. 1998; Vihavainen and Björkroth 2009).

PCR-Based DNA Fingerprinting Methods

Analysis of (fluorescent) amplified fragment length polymorphism (FAFLP or AFLP) fingerprints is another highly discriminatory characterization tool which has proven useful in the differentiation of *Leuconostoc* (De Bruyne et al. 2007) and *Weissella* species (De Bruyne et al. 2008, 2010). Furthermore, AFLP has been found valuable in typing of *O. oeni* strains (Cappello et al. 2008, 2010).

Amplified ribosomal DNA restriction analysis (ARDRA) is a technical variation of ribotyping comprising of restriction enzyme analysis of PCR amplicons from the rrn operon. Several ARDRA procedures targeting to different regions of the rrn operon have been reported; some give limited resolution being mainly applicable for rapid first-stage screening of isolates, while others provide discriminatory power allowing reliable species identification of *Leuconostocaceae*. For instance, 16S-ARDRA has been used for identification of species of *Leuconostocaceae* from grape must and wine (Rodas et al. 2003) and fermented sausages (Bonomo et al. 2008). Protocols for 16S-ARDRA employing genus-specific primers for *Weissella* (Jang et al. 2002) and *Leuconostoc* (Jang et al. 2003) have been developed to allow identification of *Weissella* and *Leuconostoc* species among other phylogenetically related lactic acid bacteria in food. Furthermore, a 16S–23S rRNA spacer ARDRA method has been developed for identification of lactic acid bacteria and proved useful in identifying *Leuconostoc* species from meat (Chenoll et al. 2003, 2007).

Fingerprinting using randomly amplified polymorphic DNA (RAPD) is another PCR-based tool applied for molecular typing of *Leuconostoc*, *Weissella*, and *O. oeni*. Various studies have demonstrated the success of RADP in monitoring *O. oeni* strains during winemaking (Bartowsky et al. 2003; Reguant and Bordons 2003; Zapparoli et al. 2000). Other workers have analyzed RAPD fingerprints to differentiate species and strain of *Leuconostoc* and *Weissella* from various sources (Aznar and Chenoll 2006; Cibik et al. 2000; De Bruyne et al. 2008; Ehrmann et al. 2009; Nieto-Arribas et al. 2010; Padonou et al. 2010).

Repetitive element palindromic PCR (REP-PCR) with the (GTG)5 primer has been applied for high-throughput screening of large collections of lactic acid bacteria isolates in numerous studies. Numerical analysis of REP-PCR patterns has been reported to be suitable for species identification and for genotypic characterization of *Leuconostoc* (Bounaix et al. 2010a; Vancanneyt et al. 2006) and *Weissella* (Bounaix et al. 2010b; Padonou et al. 2010).

DNA Sequencing-Based Analysis

Sequence analysis of 16S rRNA gene or its variable regions are widely applied strategies for classification of lactic acid bacteria and have been used for identification of *Leuconostocaceae* from various sources. In addition to 16S rRNA gene sequence analysis, phylogenetic analysis of partial sequences of several protein-coding genes such as dnaA, dnaK, gyrB, pheS, recN, rpoA, or rpoC has been reported to be highly discriminatory, allowing differentiation of species and strains within the family *Leuconostocaceae* (Arahal et al. 2008; Chelo et al. 2007; Ehrmann et al. 2009; De Bruyne et al. 2007, 2010). Furthermore, multilocus sequence typing (MLST) schemes have been proposed and applied for *O. oeni* (de las Rivas et al. 2004; Bilhere et al. 2009; Bridier et al. 2010). These studies have demonstrated that MLST is a powerful method for typing of *O. oeni* strains and provides data that can be used for studying genetic diversity, population structure, and evolutionary mechanism of this organism.

Protein Profiling

In addition to various DNA-based molecular techniques, analysis of whole-cell protein pattern by sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) has proven useful in the differentiation of closely related *Leuconostoc* and *Weissella* and has been widely applied for identification of *Leuconostocaceae* (Dicks et al. 1990; Björkroth et al. 2002; De Bruyne et al. 2007, 2008, 2010). In addition, matrix-assisted laser desorption/ionization time-of-flight mass spectrometry (MALDI-TOF MS) has been increasingly studied and applied for the identification and typing of lactic acid bacteria. This method is based on the analysis of the structural differences of microbial cells; the mass spectra mainly reflect the heterogeneity of ribosomal proteins and, thus, give a specific profile for each organism. A MALDI-TOF MS profiling method has also been reported for the family *Leuconostocaceae* (De Bruyne et al. 2011). The results have demonstrated that MALDI-TOF MS profiling is a rapid, cost-effective, and reliable method, allowing classification of most species of *Fructobacillus*, *Leuconostoc*, and *Weissella* (De Bruyne et al. 2011; Snauwaert et al. 2013).

Genomes

Within the family *Leuconostocaceae*, seven *Leuconostoc* genomes, one *Oenococcus* genome, and one *Weissella* genome have been completed (*Table 18.3*). In addition, 11 *Leuconostoc* genomes,

Table 18.3
***Leuconostocaceae* genomes**

Genome status (September 2012)	Species	Genome size	%GC	Genes	Proteins	Chromosome INSDC	Plasmid INSDC	References
Complete	*Leuconostoc carnosum* JB16	1.77	37.09	1769	1691	CP003851	CP003854 CP003852 CP003855 CP003853	Jung et al. (2012a)
Complete	*Leuconostoc citreum* KM20	1.9	38.88	1903	1820	DQ489736	DQ489738 DQ489739 DQ489740 DQ489737	Kim et al. (2008)
Complete	*Leuconostoc gasicomitatum* LMG 18811	1.95	36.7	1993	1912	FN822744	None	Johansson et al. (2011)
Complete	*Leuconostoc gelidum* JB7	1.89	36.7	1875	1796	CP003839	None	Jung et al. (2012b)
Complete	*Leuconostoc kimchii* IMSNU 11154	2.1	37.91	2209	2129	CP001758	CP001754 CP001757 CP001756 CP001753 CP001755	Oh et al. (2010)
Complete	*Leuconostoc mesenteroides* subsp. *mesenteroides* ATCC 8293	2.08	37.66	2108	2005	CP000414	CP000415	Makarova et al. (2006)
Complete	*Leuconostoc mesenteroides* subsp. *mesenteroides* J18	2.02	37.68	2020	1937	CP003101	CP003104 CP003102 CP003103 CP003105 CP003106	Jung et al. (2012c)
Complete	*Leuconostoc* sp. C2	1.88	37.9	1935	1855	CP002898	None	Lee et al. (2011c)
Complete	*Weissella koreensis* KACC 15510	1.44	35.52	1428	1357	CP002899	CP002900	Lee et al. (2011b)
Complete	*Oenococcus oeni* PSU-1	1.78	37.9	1864	1691	CP000411	None	Makarova et al. (2006)
Scaffolds or contigs	*Leuconostoc argentinum* KCTC 3773	1.72	42.9	1810	1759	AEGQ00000000	ND	Nam et al. (2010b)
Scaffolds or contigs	*Leuconostoc carnosum* KCTC 3525	3.23	40.9	ND	ND	BACM00000000	ND	Nam et al. (2011)
Scaffolds or contigs	*Leuconostoc citreum* LBAE C10	1.93	38.7	2024	1971	CAGE00000000	ND	Laguerre et al. (2012)
Scaffolds or contigs	*Leuconostoc citreum* LBAE C11	1.97	38.6	2089	2036	CAGF00000000	ND	Laguerre et al. (2012)
Scaffolds or contigs	*Leuconostoc citreum* LBAE E16	1.8	38.9	1908	1854	CAGG00000000	ND	Laguerre et al. (2012)
Scaffolds or contigs	*Leuconostoc fallax* KCTC 3537	1.64	37.5	1604	1551	AEIZ00000000	ND	Nam et al. (2010a)
Scaffolds or contigs	*Leuconostoc gelidum* KCTC 3527	1.96	36.6	1978	1928	AEMI00000000	ND	Kim et al. (2011b)
Scaffolds or contigs	*Leuconostoc lactis* KCTC 3528	2.01	42.6	2776	2727	AEOR00000000	ND	
Scaffolds or contigs	*Leuconostoc mesenteroides* subsp. *cremoris* ATCC 19254	1.64	37.9	1903	1847	ACKV00000000	ND	
Scaffolds or contigs	*Leuconostoc pseudomesenteroides* 4882	2.01	39.1	2152	2086	CAKV00000000	ND	Meslier et al. (2012)

Table 18.3 (continued)

Genome status (September 2012)	Species	Genome size	%GC	Genes	Proteins	Chromosome INSDC	Plasmid INSDC	References
Scaffolds or contigs	*Leuconostoc pseudomesenteroides* KCTC 3652	3.24	38.3	3888	3832	AEOQ00000000	ND	Kim et al. (2011a)
Scaffolds or contigs	*Weissella cibaria* KACC 11862	2.32	ND	2234	2154	AEKT00000000	ND	Kim et al. (2011c)
Scaffolds or contigs	*Weissella confusa* LBAE C39-2	2.28	ND	2237	2156	CAGH00000000	ND	Amari et al. (2012b)
Scaffolds or contigs	*Weissella koreensis* KCTC 3621	1.73	35.5	1750	1672	AKGG00000000	ND	Lee et al. (2012a)
Scaffolds or contigs	*Weissella paramesenteroides* ATCC 33313	1.96	37.9	2020	1952	ACKU00000000	ND	
Scaffolds or contigs	*Weissella thailandensis* fsh4-2	ND	40.0	1651	1437			
	HE575133NDHE575182	ND				Benomar et al. (2011)	Scaffolds or contigs	
Oenococcus kitaharae DSM 17330	1.84	42.7	1878	1825		CM001398	CM001399	Borneman et al. (2012a)
Scaffolds or contigs	*Oenococcus oeni* ATCC BAA-1163	1.75	37.9	1678	1398	AAUV00000000	ND	
Scaffolds or contigs	*Oenococcus oeni* AWRIB202	ND	ND	1831	1732	AJTO00000000	ND	Borneman et al. (2012b)
Scaffolds or contigs	*Oenococcus oeni* AWRIB304	1.85	37.9	1844	1743	AJIJ00000000	ND	Borneman et al. (2012b)
Scaffolds or contigs	*Oenococcus oeni* AWRIB318	1.81	37.9	1798	1698	ALAD00000000	ND	Borneman et al. (2012b)
Scaffolds or contigs	*Oenococcus oeni* AWRIB418	1.84	37.8	1817	1739	ALAE00000000	ND	Borneman et al. (2012b)
Scaffolds or contigs	*Oenococcus oeni* AWRIB419	1.79	37.8	1780	1685	ALAF00000000	ND	Borneman et al. (2012b)
Scaffolds or contigs	*Oenococcus oeni* AWRIB422	1.81	37.9	1812	1696	ALAG00000000	ND	Borneman et al. (2012b)
Scaffolds or contigs	*Oenococcus oeni* AWRIB429	1.93	37.9	2161	2161	ACSE00000000	ND	Borneman et al. (2010)
Scaffolds or contigs	*Oenococcus oeni* AWRIB548	1.84	37.9	1831	1713	ALAH00000000	ND	Borneman et al. (2012b)
Scaffolds or contigs	*Oenococcus oeni* AWRIB553	1.76	37.7	1733	1645	ALAI00000000	ND	Borneman et al. (2012b)
Scaffolds or contigs	*Oenococcus oeni* AWRIB568	1.87	38.0	1879	1778	ALAJ00000000	ND	Borneman et al. (2012b)

Table 18.3 (continued)

Genome status (September 2012)	Species	Genome size	%GC	Genes	Proteins	Chromosome INSDC	Plasmid INSDC	References
Scaffolds or contigs	*Oenococcus oeni* AWRIB576	1.88	38.0	1873	1774	ALAK00000000	ND	Borneman et al. (2012b)
Scaffolds or contigs	*Oenococcus oeni* DSM 20252	ND	ND	1705	1616	AJTP00000000	ND	Borneman et al. (2012b)
Scaffolds or contigs	*Fructobacillus fructosus* KCTC 3544	1.47	44.6	1600	1550	AEOP00000000	ND	

INSDC International Nucleotide Sequence Database Collaboration
ND no data

14 *Oenococcus* genomes, five *Weissella* genomes, and one *Fructobacillus* genome are available as draft genomes made up of a few to many contigs. From genome mapping, the genome size of *Leuconostocaceae* genomes has been estimated to range in size from 1.4 to 2.2 Mb (Chelo et al. 2010), and all completely sequenced genomes also fall within that size range. As noted previously, most *Leuconostocaceae* strains do contain plasmids, although spontaneous curing of plasmids frequently occurs when these strains are maintained in laboratory conditions (Brito and Paveia 1999).

The analysis of the pan genomes within the homogeneous genera *Fructobacillus*, *Leuconostoc*, *Oenococcus*, and *Weissella* has shown that the core genome within one species comprises between 67 % and 80 % of a genome (Borneman et al. 2012b; Johansson et al. 2011). This is in agreement with the core genome proportion of 60 % in the highly divergent species *Lactobacillus casei* (Broadbent et al. 2012). The size of the supragenome for a species is directly proportional to number of sequenced strains until a saturation level is reached. The saturation level corresponds to the size of the complete supragenome and can be calculated when sufficient number of strains have been sequenced (Boissy et al. 2011). The size of the supragenomes characterized for LAB species is two to three times of the size of any individual genome (Boissy et al. 2011; Borneman et al. 2012b; Broadbent et al. 2012).

It has been shown that there is a good correlation between experimentally determined DNA–DNA hybridization (DDH) and digital DDH, calculated from sequence alignment of the genome sequences (Konstantinidis and Tiedje 2005; Auch et al. 2010). This is also the case for the genomes of *Leuconostocaceae*, although the genomes and experimental DDH are not obtained from the same strains in all cases.

All fully sequenced *Leuconostocaceae* genomes contain complete or partial prophages. The prophages of *Oenococcus* have been well characterized (São-José et al. 2004), and they all use tRNA genes as attachment sites in the genome (Borneman et al. 2012b). Genomes from *Fructobacillus* and *Leuconostoc* all have four rrn operons, while genomes from *Oenococcus* have two rrn operons. *Weissella* have previously been shown to have between six and eight rrn operons (Chelo et al. 2010), but the only completed *Weissella* genome, *W. koreensis*, actually have five rrn operons. The rrn operons are usually distributed around the chromosome, except for *L. gasicomitatum* and *L. gelidum*, where all four rrn operons are concentrated on the last quarter of the chromosome.

Phenotypic Analyses

Leuconostocaceae are Gram positive, asporogenous, nonmotile (with the exception of *Weissella beninensis*), chemoorganotrophic, facultative anaerobic, and catalase negative. They are unable to reduce nitrate and grow in rich media supplemented with growth factors and amino acids. *Leuconostocaceae* generate energy by substrate-level phosphorylation. Glucose is fermented heterofermentatively via 6-phosphogluconate/phosphoketolase pathway yielding lactic acid, CO_2, ethanol, and/or acetate. Glucose-6-phosphate dehydrogenase and xylulose-5-phosphoketolase are the key enzymes of the pathway (Garvie 1986). Earlier it was thought that *Leuconostocaceae* do not have enzyme fructose 1,6-biphosphate aldolase required for homolactic fermentation, but the genomic analyses have shown that the genes encoding this enzyme are relatively common within the family. The main morphological, metabolic, and chemotaxonomic characters of the genera of *Leuconostocaceae* are shown in *Table 18.4*.

Leuconostoc[AL] van Tieghem (1878), 198[AL] emend. mut. char. Hucker and Pederson (1930), 66[AL]

Leuconostoc cells are spherical to ellipsoidal but may also resemble short rods, especially when grown in glucose medium or on solid medium. Cells are often seen in pairs or short chains.

Table 18.4
Morphological, metabolic, and chemotaxonomic characters of genera of *Leuconostocaceae*

	Leuconostoc	*Weissella*	*Oenococcus*	*Fructobacillus*
Morphology	Spherical to ellipsoidal	Ellipsoidal to short rods	Spherical to ellipsoidal	Rods
Lactic acid enantiomer from glucose	D(−)	D(−) or DL	D(−)	D(−)
Hydrolysis of arginine	−	+/−	−	−
Dextran from sucrose	−/+	−/+	−	−
Growth in 10 % ethanol	−	−	+/−	−
Peptidoglycan	L-Lys-L-Ser-L-Ala_2 or L-Lys- L-Ala_2	L-Lys-L-Ala_2 or L-Lys-L-Ala or L-Lys-L-Ala-Gly-L-Ala_2 or L-Lys-L-Ala-L-Ser	L-Lys-L-Ala-L-Ser or L-Lys-L-Ser_2	L-Lys-L-Ala
Major fatty acids	C14:0, C16:0, C16:1(9), C18:1(9), C19cycl(9)	C14:0, C16:0, C16:1(9), C17:0, C18:0, C18:1(9), C19cycl(9), C19cycl(11)	C16:0, C16:1(9), C18:1(9), C18:1(11), C19cycl(9), C19cycl (11)	C16:0, C16:1(9), C18:1(9), C18:1(11)
G+C content of DNA (Mol%)	36–45	37–47	37–43	42–45

Abbreviations: *Lys* lysine, *Ala* alanine, *Ser* serine, *Gly* glycine, *ND* no data
Symbols: + positive reaction, − negative reaction, +/− mostly positive, only some strains negative, and −/+ mostly negative, only some strains positive

True cellular capsules are not formed. Some strains produce extracellular dextran, which forms an electron-dense coat on the cell surface.

Leuconostocs develop visible colonies usually only after three to five days of incubation at 25–30 °C. Colonies on commonly used LAB media are smooth, round, grayish white, and less than 1 mm in diameter. Unlike other leuconostocs, most of the *Leuconostoc citreum* strains are able to form yellow-pigmented colonies (Farrow et al. 1989).

The optimal growth temperature is between 20 °C and 30 °C, although most species are able grow at 37 °C. Growth at 4 °C or below has been reported for *L. gelidum*, *L. carnosum*, and *L. gasicomitatum* (Holzapfel et al. 2009). Some psychrotrophic strains grow poorly at 30 °C (Björkroth et al. 2000). Leuconostocs are non-acidophilic and prefer an initial medium pH of 6.5. Most of the species are unable to grow at pH 4.8. Growth is uniform, except when cells in long chains sediment. In stab cultures, growth is concentrated in the lower two thirds. Growth on surface plates is poor under aerobic conditions, but is stimulated when incubated anaerobically.

All leuconostocs produce predominantly D(−) enantiomer lactic acid from glucose and are unable to hydrolyze arginine. *Leuconostoc* species are difficult, sometimes impossible, to distinguish by phenotypic routine testing. Many reactions are strain dependent or are, on the other hand, shared between the different species (*Table 18.1*). Only *L. mesenteroides* subsp. *cremoris* can be easily distinguished from the other leuconostocs owing to its poor carbohydrate fermentation capability. Sugars most helpful for the differentiation of *Leuconostoc* species are L-arabinose, melibiose, and D-xylose.

Leuconostoc spp. metabolize glucose heterofermentatively via 6-phosphogluconate/phosphoketolase pathway, yielding lactic acid, CO_2, ethanol, and/or acetate. Characteristics to the pathway are that hexoses are initially oxidized to pentoses resulting in generation of NAD(P)H. Under anaerobic conditions, NAD+ is regenerated by reduction of acetyl-CoA to ethanol in a process that does not produce ATP. However, if other means to oxidize NAD(P)H are available, acetyl-CoA can be converted to acetate which doubles the amount ATP produced per unit of hexose consumed. In the presence of oxygen, strains of *L. mesenteroides* use NADH oxidases and NADH peroxidases as alternative mechanisms to regenerate NAD+ (Condon 1987). Leuconostocs are also able to re-oxidize NAD(P)H by using pyruvate, fructose, or citrate as electron acceptors. The cofermentation of several metabolites increases the production of ATP and, subsequently, the growth rate (Zaunmüller et al. 2006). Citrate metabolism was also reported to form proton motive force across the cell membrane in *L. mesenteroides* (Marty-Teysset et al. 1996) which may contribute to the enhanced growth.

Most *Leuconostoc* species have genes encoding *bd*-type cytochrome oxidase, and they do respire in the presence of heme and oxygen (Brooijmans et al. 2009; Johansson et al. 2011; Sijpesteijn 1970). Respiration enables higher biomass production than fermentation (Brooijmans et al. 2009).

Under reducing conditions, leuconostocs may ferment citrate and hexose to diacetyl and acetoin which are important flavor compounds in dairy products. The amount of diacetyl produced is strain dependent (Walker and Gilliland 1987). In a study by Schmitt et al. (1997), *Leuconostoc mesenteroides* subsp. *mesenteroides* produced diacetyl as a result of cofermentation of

xylose and citrate but not from glucose and citrate. Xylose reduced the activity of lactate dehydrogenase in comparison to glucose, meaning that less pyruvate was converted to lactate in the presence of xylose. Instead, pyruvate was converted to diacetyl/acetoin. In comparison to glucose, xylose may reduce lactate dehydrogenase activity because generation of pyruvate from xylose generates less NAD(P)H, meaning that less reducing power is available for the formation of lactate from pyruvate, a reaction catalyzed by lactate dehydrogenase. Instead of diacetyl/acetoin, surplus pyruvate formed from citrate could be also converted to acetic acid with a coupled generation of ATP, but this pathway seems not to be beneficial under acidic conditions (Schmitt et al. 1997).

Fermentation of pentoses via phosphogluconate/phosphoketolase pathway generates less NAD(P)H than fermentation of hexoses. Thus, acetyl-CoA produced from pentoses can be converted to acetate without a need of an external electron acceptor for the regeneration of NAD+. Despite the supposed benefits of pentose fermentation, many *Leuconostoc* species seem to be unable to ferment the common pentoses L-arabinose, ribose, or D-xylose, when provided as the sole carbon source (*Table 18.1*). The reason for this is not known. Some leuconostocs are able to co-metabolize pentoses together with other carbon sources, e.g., xylose together with citrate (Schmitt et al. 1997).

Fructose is fermented by all *Leuconostoc* spp., except by some strains of *L. mesenteroides* subsp. *cremoris*. If fructose is used as an electron acceptor, mannitol is formed. The regeneration of NAD(P)H by fructose enables the production of acetate instead of ethanol which results in gain of ATP and enhanced growth. Interestingly, this process has been investigated as a means to produce D-mannitol from fructose by leuconostocs at industrial scale (Kiviharju and Nyyssölä 2008; von Weymarn et al. 2003).

Citrate and malate are the organic acids most frequently fermented by *Leuconostoc* spp. Acetate and tartrate are not utilized. Malate is converted into L(+)-lactate and CO_2 by *L. mesenteroides* subsp. *mesenteroides*. Leuconostocs do not metabolize sugar alcohols other than mannitol. Glycogen and starch are generally not degraded with the exception of *L. miyukkimchii* that is able to metabolize starch (Lee et al. 2012b).

Many leuconostocs are able to form dextran from sucrose, and this property has been used as one criterion differentiating the species. However, dextran production among *L. gelidum* and *L. carnosum* is strains dependent. The ability to form dextran is often lost when serial transfers are made in media of increasing salt concentrations (Pederson and Albury 1955). Dextran production from sucrose is dependent on the growth medium (Pederson and Albury 1955).

Little is known about the production of biogenic amines by leuconostocs. No tyramine formation was detected in strains of *Leuconostoc* isolated from fresh- and vacuum-packaged meat (Edwards et al. 1987). Some strains of *L. mesenteroides* subsp. *mesenteroides*, subsp. *cremoris*, and *Leuconostoc paramesenteroides* are known to produce tyramine and tryptamine (Bover-Cid and Holzapfel 1999; de Llano et al. 1998; Moreno-Arribas et al. 2003).

The major fatty acids recorded for *Leuconostoc* spp. are myristic (C14:0), palmitic (C16:0), palmitoleic [C16:1(9)], oleic [C18:1(9)], and dihydrosterculic acid [C19-cyc(9)] (Schmitt et al. 1989; Shaw and Harding 1989; Tracey and Britz 1989). *Leuconostoc* spp. differ from *Oenococcus* spp. and *Fructobacillus* spp. in containing oleic acid, and not vaccenic [C18-1(11)] acid, as the dominant C18:1 fatty acid (Tracey and Britz 1989). *L. carnosum* and *L. gelidum* are clearly differentiated based on their fatty acid profiles (Shaw and Harding 1989).

The interpeptide bridge of the peptidoglycan in leuconostocs consists either Lys-Ser-Ala_2 or Lys-Ala_2.

Weissella[VP] Collins et al. (1993, 595); emend. Padonou et al. (2010)

The genus *Weissella* harbors two different morphological types: the short rods and the ovoid-shaped cocci. Some strains, e.g., in *W. minor*, are pleomorphic. *Weissella* colonies are 1–2 mm in diameter, white to creamish white, smooth, circular, and convex after 3–4 days of anaerobic growth. Weissellas are nonmotile with the exception of *W. beninensis*, the only motile species belonging to *Leuconostocaceae*. *W. beninensis* has peritrichous flagella (Padonou et al. 2010).

Weissellas are heterofermentative lactic acid bacteria and share most of the metabolic properties with leuconostocs. Unlike leuconostocs, some *Weissella* species produce DL lactic acid from glucose (*Table 18.2*). Most weissellas are able to hydrolyze arginine. Growth occurs at 15 °C, with some species growing at 42–45 °C. All species are able to grow at 37 °C and most species are able to grow at pH 4.8.

Phenotypic tests have been traditionally used to identify *Weissella* species. Cell morphology has some diagnostic value. Hydrolysis of arginine is a simple biochemical test for differentiation. A battery of ten sugars was recommended by Collins et al. (1993) to be used in combination with other phenotypic tests for identification. Among some weissellas, and particularly *W. confusa*, dextran production appears to be a common and a widespread feature.

Similar to leuconostocs, some weissellas have genes encoding *bd*-type cytochrome oxidase required for heme-dependent respiration (Kim et al. 2011c), but functional respiration chain is yet to be reported for weissellas.

Literature describing the production of biogenic amines by *Weissella* spp. is scarce. *Weissella halotolerans* W22 combines an arginine deaminase pathway and an ornithine decarboxylation pathway, which results in generation of biogenic amine putrescine and proton motive force (Pereira et al. 2009).

The cell wall peptidoglycan in weissellas is based on lysine as dipeptide, and, with the exception of *W. kandleri*, all contain alanine or alanine and serine in the interpeptide bridge. In addition, the interpeptide bridge of *W. kandleri* (Lys-L-Ala-Gly-L-Ala_2) contains glycine (Holzapfel and Van Wyk 1982).

Fatty acid profiles can be used to differentiate weissellas. Applying a rapid gas chromatographic method, Samelis et al. (1998) could differentiate between *W. viridescens*, *W. paramesenteroides*, *W. hellenica*, and some typical arginine-negative *Weissella* isolates from meats on the basis of their cellular fatty acid

Table 18.5
Phenotypic characteristics of *Fructobacillus* spp. *and Oenococcus* spp.

Characteristics	*F. fructosus*	*F. durionis*	*F. ficulneus*	*F. pseudoficulneus*	*F. tropaeoli*	*O. oeni*	*O. kitaharae*
Acid from							
Galactose	–	–	–	–	–	d	+
Maltose	–	(+)	w	–	–	–	+
Mannose	–	–	–	–	–	d	+
Mannitol	(+)	(+)	(+)	(+)	(+)	–	–
Melibiose	–	–	–	–	–	d	+
Sucrose	–	+	w	–	–	–	–
Trehalose	–	(+)	(+)	–	–	+	+
Turanose	–	+	w	–	–	ND	ND
Ammonia from arginine	–	–	–	–	ND	d	ND
Hydrolysis of aesculin	–	–	–	–	–	+	ND
Peptidoglycan type	Lys-Ala	ND	Lys-Ala	ND	ND	Lys-Ala-Ser or Lys-Ser_2	ND
Cell morphology	Rods	Rods	Rods	Rods	Rods	Coccoid to elongated cocci	Small ellipsoidal cocci
References	Endo et al. (2011)	Endo et al. (2011)	Endo et al. (2011)	Endo et al. (2011)	Endo et al. (2011)	Dicks et al. (1995)	Endo and Okada, (2006)

+, 90 % or more of strains positive; –, 90 % or more of strains negative; d, 11–98 % of strains positive; (), delayed reaction; w, weakly positive
ND no data

composition. *W. viridescens* synthesized eicosenoic (C20:1) acid, while the other two species did not. Unlike *W. paramesenteroides*, *W. hellenica* and *W. viridescens* contained zero to low amounts of cyclopropane fatty acids with 19 carbon atoms, i.e., dihydrosterculic [C19cycl(9)], or lactobacillic acid [C19cycl(11)].

Oenococcus[VP] Dicks et al. (1995) emend. Endo and Okada (2006)

Oenococcus species are Gram positive and nonmotile, ellipsoidal to spherical in shape. Growth in broth is slow and usually uniform. Colonies usually develop only after 5 d and are less than 1 mm in diameter.

The optimal growth temperature is between 20 °C and 30 °C. Oenococci prefer anaerobic conditions for growth. They produce D-(−)-lactate, CO_2, and ethanol or acetate from glucose (*Table 18.5*) via a pathway not yet fully elucidated. In most species, both NAD and NADP may serve as coenzymes of the glucose-6-phosphate dehydrogenase, but in *O. oeni*, only NADP is required (Garvie 1975). Fermentation profiles of the different *O. oeni* strains vary greatly despite the genetically homogeneous nature of this species.

O. oeni is an important organism for malolactic fermentation (MLF) in wine and has several specific characteristics to inhabit in wine, e.g., acidophile and the ability to grow in medium containing 10 % of ethanol. These characteristics differentiate *O. oeni* from other *Leuconostocaceae*, including *O. kitaharae*. *O. kitaharae* is not acidophilic, cannot tolerate 10 % ethanol, and does not perform MLF (Endo and Okada 2006).

The citrate metabolism in *O. oeni* is conducted only when fermentable carbohydrates (e.g., glucose) are available. The cofermentation of citrate and glucose in *O. oeni* is physiologically important for the organism, as co-metabolism of citrate–glucose enhances the ATP synthesis and, consequently, increases the growth rate and biomass yield (Ramos and Santos 1996; Liu 2002).

O. kitaharae does not perform MLF. A stop codon has been found in the gene encoding malolactic enzyme in *O. kitaharae* (Borneman et al. 2012a; Endo and Okada 2006).

Some *O. oeni* strains may produce biogenic amines in wine (Bonnin-Jusserand et al. 2011; Izquierdo Cañas et al. 2009; Lucas et al. 2008). Gardini et al. (2005) reported tyramine formation by a strain of *O. oeni* isolated from Italian red wine. The formation of putrescine from arginine by some strains could be demonstrated (Guerini et al. 2002). However, e.g., Moreno-Arribas et al. (2003) could not detect any potential among *O. oeni* strains to form biogenic amines. Production of histamine by *O. oeni* has been extensively analyzed with contradictory results (Garcia-Moruno and Muñoz 2012).

Eighteen fatty acids are associated with *O. oeni* (Tracey and Britz 1987, 1989). The numerical analysis of the fatty acids

showed four clusters defined at $r = 0.920$, with five strains unassigned. On the basis of the amounts of oleic acid [C18-1(9)] and C19-cyclopropane fatty acids, the strains of *O. oeni* could also be distinguished from each other. For the majority of *O. oeni* strains, the result obtained with the cellular fatty acid analysis confirmed the phenotypic relationships.

Fructobacillus[VP] Endo and Okada (2008)

Fructobacilli are Gram-positive and nonmotile rods. They produce lactate, acetate, CO_2, and trace amounts of ethanol from glucose (Table 18.5). Produced lactate is mainly D-isomer. *Fructobacillus* species prefer fructose over glucose as a carbon source. Aerobic culturing or the presence of pyruvate enhances their growth on glucose (Endo and Okada 2008). Because of the characteristics, they are classified as fructophilic LAB (Endo et al. 2009, 2011). They are usually osmotolerant and grow with 30 % (w/v) fructose, except *F. tropaeoli*. *Fructobacillus* spp. are usually poor sugar fermenters, and some of them metabolize only fructose, glucose, and mannitol. On the agar medium, they do not grow on glucose under anaerobic conditions if external electron acceptors are not supplied.

The cell wall peptidoglycan type of *F. ficulneus* is A3α. The predominant fatty acids in *F. ficulneus* and *F. fructosus* are C16:1(9), C16:0, C18:1(9), and C18:1(11) (Antunes et al. 2002).

Isolation, Enrichment, and Maintenance Procedures

Leuconostoc and *Weissella*

Leuconostoc and *Weissella* are isolated using rich media such those routinely used for culturing lactic acid bacteria, including All-Purpose Tween (Evans and Niven 1951), MRS (De Man et al. 1960), and Rogosa SL (Rogosa et al. 1951). A review by Schillinger and Holzapfel (2011) discusses in detail the selective and semi-selective media available and applied for isolation of lactic acid bacteria from different habitat such as meat or dairy products. If psychrotrophic species, such as *L. carnosum*, *L. gasicomitatum*, *L. gelidum*, and *L. inhae*, are expected to occur in the sample, an incubation temperature of 25 °C is recommended. For cultures on solid medium, an anaerobic atmosphere is recommended, while liquid cultures can be maintained in aerobic conditions.

Overall, neither selective agents nor growth conditions have been identified that allow growth and selective isolation of *Leuconostoc* or *Weissella* while inhibiting other lactic acid bacteria. Although selective and differential media for detection and enumeration of *Leuconostoc* have been proposed, they may give unreliable results in cases of samples with large numbers of *Pediococcus* and *Lactobacillus* which share many physiological and metabolic properties with *Leuconostoc* spp. Inclusion of vancomycin (30 μg/mL) in a growth medium may assist the selective isolation of *Leuconostoc* and *Weissella* from mixed bacterial populations. However, as some *Pediococcus* and *Lactobacillus* spp. are also resistant to vancomycin, this strategy is not entirely selective, and the identities of the isolates recovered need to be confirmed.

Oenococcus

O. oeni is well known to need a specific growth factor. Tomato juice or grape juice is usually added to the medium to supply the growth factor. The pH of the medium is set at 4.8, as the species has a unique acidophilic characteristic. The species hardly grow under aerobic conditions and prefer anaerobic conditions. Several media have been developed to isolate because of the importance of the species in industry, and acidic tomato broth (ATB) might be one of the most well-used medium for isolation and culture of *O. oeni* (Garvie 1967b; Garvie and Mabbitt 1967). Björkroth and Holzapfel (2006) have summarized the several media for isolation of *O. oeni* from wine.

O. kitaharae has growth characteristics different from those of *O. oeni*. Tomato juice or grape juice does not favor the growth of *O. kitaharae*, and low pH prevents its growth. The organism needs a medium rich in nutrients and anaerobic conditions for maximum growth (Endo and Okada 2006). It was originally isolated using MRS agar containing inhibitors of aerobic fungi (sodium azide and cycloheximide). The growth was very slow and weak in MRS broth and MRS agar. Additional nutrients, e.g., half-strength brain heart infusion (BHI) broth, and anaerobic conditions are required to enhance the growth rate and biomass yield of this bacterium.

Fructobacillus

As *Fructobacillus* species possess very unique physiological characteristics, selective enrichment isolation can be conducted (Endo et al. 2009). *Fructobacillus* species prefer fructose over glucose and grow very slowly on glucose under static conditions. They cannot metabolize glucose under anaerobic conditions. However, the presence of external electron acceptors, e.g., pyruvate or oxygen, enhances the growth of *Fructobacillus* species. Thus, enrichment culturing on fructose, e.g., FYP broth (Endo et al. 2009), under aerobic conditions favors their growth, as other LAB usually prefer anaerobic conditions. To inhibit the growth of aerobic bacteria and fungi in enrichment broth, sodium azide and cycloheximide are very useful. The enrichment can be streaked onto the FYP agar and incubated under aerobic conditions for further selection. Certain oxygen-tolerant LAB, e.g., *Lactobacillus plantarum*, *L. brevis*, and *Leuconostoc* spp., may grow as well, but they can be easily differentiated from *Fructobacillus* species based on the poor glucose utilization of *Fructobacillus* species. Because of their unique characteristics, *Fructobacillus* species are regarded as fructophilic LAB.

Differentiation of *Fructobacillus* species from *Lactobacillus kunkeei*, which is also a fructophilic species, requires carbohydrate fermentation patterns or molecular approaches.

Maintenance Procedures

Most cultures on liquid or solid media remain viable for at least two to three weeks at 4–6 °C. Longer maintenance is in glycerol (10–20 % v/v) or dimethyl sulfoxide (10 % v/v) suspension at −20° (for months) or preferably at −70 °C or lower (for several years). Cultures are also well preserved in liquid nitrogen or by lyophilization (freeze-drying).

Ecology

Leuconostocs are associated with plants and decaying plant material. They have been detected in green vegetation and roots (Hemme and Foucaud-Scheunemann 2004; Mundt 1967) and in various fermented vegetable products, such as cucumber, kimchi, cabbage, and olives (Kim and Chun 2005; Mäki 2004). In addition to plant-originated material, leuconostocs are frequent in foods of animal origin, including raw milk and dairy products, meat, poultry, and fish (Kim and Chun 2005; Björkroth and Holzapfel 2006). However, healthy warm-blooded animals, including humans, are rarely reported to carry *Leuconostoc* in the microbiota of their gut or mucous membranes, whereas leuconostocs have been recovered from the intestines of fish (Williams and Collins 1990).

L. carnosum, *L. gasicomitatum*, and *L. gelidum* have often been associated with food spoilage (Schillinger et al. 2006). Some modified atmosphere packaged meat- and vegetable-based foods have been prone to leuconostoc spoilage manifesting as bulging of the packages, off-odors and smells, and color changes. In addition to the publications cited in this paragraph, leuconostocs have been frequently reported to belong to microbiota of various fermented foods (see section ❯ Application).

O. oeni usually predominates at the end and after alcoholic fermentation in fermenting wine and plays a key role in the MLF. This is because of high resistance to SO_2 and ethanol in the organism as compared to other bacteria. SO_2 is added to wine as an antioxidant and to prevent the growth of undesirable microorganisms (Amerine et al. 1980). In the work by Carreté et al. (2002), the presence of 2 mM of SO_2 had no impact on MLF by *O. oeni*, but 5 mM of SO_2 caused considerable delay on MLF. Cell growth is not necessary to conduct MLF (Carreté et al. 2002). *O. oeni* is also a responsible organism for MLF in ciders (Sánchez et al. 2012). The cider isolates were separated from wine isolates based on the results of MANOVA analysis of PFGE (Bridier et al. 2010). This is generally supported by MLST (Bridier et al. 2010), suggesting that *O. oeni* strains have had habitat-specific evolution. Quite recently, an interesting study which found DNA of *O. oeni* in cocoa bean fermentation by metagenomic approach was reported (Illeghems et al. 2012).

O. kitaharae was originally isolated from a compost of distilled *shochu* residue in Japan (Endo and Okada 2006). The species was also isolated from the wastewater of a starch factory in Japan (Dr. Tomohiro Irisawa, personal communication). The preferred habitat of *O. kitaharae* is still uncertain, but compost, wastewater, sludge, and sewage are possible niches.

The habitats of *Weissella* species are variable and the sources of isolation suggest environmental (soil, vegetation) origin. *W. viridescens*, *W. halotolerans*, and *W. hellenica* have been associated with meat and meat products. *W. viridescens* may cause spoilage of cured meat due to green discoloration (Niven and Evans 1957), and it also is a prevailing spoilage LAB in Spanish blood sausage called Morcilla de Burgos (Koort et al. 2006; Diez et al. 2009; Santos et al. 2005). *W. viridescens* is considered somewhat heat resistant (Niven et al. 1954) which is not a common property for a LAB.

W. cibaria, *W. confusa*, *W. koreensis*, and *W. oryzae* have been detected in fermented foods of vegetable origin (Björkroth et al. 2002; Lee et al. 2002), whereas *W. confusa* has been associated with Greek salami (Samelis et al. 1994), Mexican pozol (Ampe et al. 1999), and Malaysian chili bo (Leisner et al. 1999). *Weissella cibaria* and *W. confusa* have also been associated with various types of sour doughs (Galle et al. 2010; Katina et al. 2009; Scheirlinck et al. 2007; De Vuyst et al. 2002). *W. soli* (Magnusson et al. 2002) is the only species known to originate in soil, but *W. paramesenteroides* has also been detected in soil (Chen et al. 2005). In addition, weissellas have been isolated from sediments of a coastal marsh (Zamudio-Maya et al. 2008) and lake water (Yanagida et al. 2007).

W. ghanensis, *W. fabaria*, and *W. fabalis* were detected in traditional heap fermentations of Ghanaian cocoa bean (De Bruyne et al. 2008, 2010; Snauwaert et al. 2013). *W. beninensis* (Padonou et al. 2010) originates from submerged fermenting cassava. Weissellas in food fermentations are further discussed in section "❯ Application" of this chapter.

W. ceti was isolated from beaked whales (Mesoplodon bidens); nine isolates were obtained from different organs of four animals (Vela et al. 2011).

Fructobacillus species can be found in several fructose-rich niches, e.g., fresh flowers and fruits. *F. fructosus* and *F. tropaeoli* were originally isolated from fresh flowers (Kodama 1956; Endo et al. 2011), and *F. ficulneus* and *F. pseudoficulneus* were originally found in ripe figs (Antunes et al. 2002; Chambel et al. 2006). Endo et al. (2009) also isolated a *F. fructosus* strain from a flower and *F. pseudoficulneus* strains from a banana peel and a fig. Moreover, *Fructobacillus* species have been found in several fermented foods produced from fruits. *F. durionis* was originally isolated from *tempoyak*, a Malaysian acid-fermented condiment made from the pulp of the durian fruit (Leisner et al. 2005). Several *Fructobacillus* species have been found in cocoa bean fermentation (Nielsen et al. 2007; Papalexandratou et al. 2011a, b) and wine (Mesas et al. 2011). Moreover, *F. fructosus* has been found from guts of several fructose-related insects, i.e., bumblebees, fruit flies, and giant ants (He et al. 2011; Koch and Schmid-Hempel 2011; Thaochan et al. 2010). This is highly interesting as *Fructobacillus* species do not grow on glucose under anaerobic conditions. They can grow well on fructose under anaerobic conditions.

Pathogenicity and Clinical Significance

Some *Leuconostoc* species have caused infections, but most of the patients had received vancomycin, had an underlying disease, or were premature babies. These bacteria are not a risk for healthy individuals, and leuconostocs are considered as GRAS organisms (Schillinger et al. 2006). All leuconostocs are intrinsically resistant to vancomycin and other glycopeptide antibiotics; the first clinical reports were published in 1984–1985 (Buu-Hoi et al. 1985; Huygens 1993; Orberg and Sandine 1984: Elisha and Courvalin 1995).

W. confusa has been detected in the normal human intestinal microbiota (Stiles and Holzapfel 1997; Walter et al. 2001; Tannock et al. 1999). *W. cibaria* and *W. confusa* have been detected in clinical samples of humans and animals (Björkroth et al. 2002). *W. confusa* has been associated with bacteremia (Olano et al. 2001; Harlan et al. 2011; Salimnia et al. 2011; Lee et al. 2011a) and endocarditis (Flaherty et al. 2003) in humans. As in the case of *Leuconostoc* infection, the infection is mainly due to the natural resistance of these species to vancomycin and an underlying disease or immunosuppression of the host. In addition to human cases, *W. confusa* has been documented as a cause for a systemic infection in a non-immunocompromised primate (*Cercopitheus mona*) (Vela et al. 2003), and unknown *Weissella* strains were isolated from a diseased rainbow trout in China (Liu et al. 2009).

Oenococcus and *Fructobacillus* species have not been associated with disease in humans or animals.

Application

Meat

As commercial starter organisms for meat fermentations, leuconostocs are not as important as some *Lactobacillus* and *Pediococcus* spp. (Holzapfel 1998). However, leuconostocs and weissellas are repeatedly found in fermented meat products (Albano et al. 2009; Aymerich et al. 2006; Babic et al. 2011; Ben Belgacem et al. 2009; Benito et al. 2007; Danilovic et al. 2011; Kesmen et al. 2012; Papamanoli et al. 2003; Parente et al. 2001; Samelis et al. 1994; Tu et al. 2010), although at lower levels than lactobacilli. *L. mesenteroides* and *W. viridescens* are the species most often encountered in fermented meats, but *L. carnosum*, *L. gelidum*, *L. pseudomesenteroides*, *W. confusa*, and *W. paramesenteroides* are also reported. Weissellas and leuconostocs are associated with the production of bacteriocins (Hastings et al. 1994) which could be of importance in the fermentation process and may contribute to the microbiological safety of the final product.

Dairy

In contrast to the lactococci, leuconostocs are not competitive growers or important producers of lactic acid in milk. The ability of certain strains to produce the flavor compound diacetyl, however, has led to their frequent incorporation into mixed strain starter cultures in products like buttermilk, butter, and quarg (cream cheese). Leuconostocs form functional associations with lactococci that ferment lactose efficiently to lactate. The subsequent acidification creates favorable conditions for the production of diacetyl from citrate by citrate-lyase-positive *Leuconostoc* strains (Vedamuthu 1994). Strain 91404 of *L. mesenteroides* subsp. *cremoris* was selected by Levata-Jovanovic and Sandine (1997) as an aroma producer in the preparation of experimental cultured buttermilk on the basis of its low diacetyl reductase activity, citrate utilization, and high diacetyl production under acidic conditions, and also because of its growth characteristics and its compatibility with *Lactococcus* strains. Fortification of ripened buttermilk with sodium citrate resulted in a significant increase of diacetyl and acetoin production during buttermilk storage at 5 °C for 2 weeks. Surplus of citrate, low pH of 4.5–4.7, a sufficient number of active, non-growing aroma producers, air incorporation during curd breaking, and low storage temperatures stimulated citrate metabolism and enhanced flavor during the 2 weeks of storage. Optimal development of *L. mesenteroides* subsp. *cremoris* appears to be dependent on the manganese content of the milk, and with values <15 μg/L, it may be outcompeted in a mixed strain starter culture. The ratio of *L. mesenteroides* subsp. *cremoris* to *Lactococcus lactis* in mixed culture is also dependent on the incubation temperature: warmer than 25 °C favors *L. lactis* (Hemme and Foucaud-Scheunemann 2004).

L. mesenteroides subsp. *cremoris* plays an important role in the desired CO_2 formation in the cheeses such as Gouda and Edam where it comprises ca. 5 % of a typical starter culture, as compared to 2–3 % for Tilsiter (Zickrick 1996). Cogan et al. (1997) studied 4,379 isolates from 35 artisanal dairy products, including 24 artisanal cheeses, and identified 10 % of the LAB strains as *Leuconostoc* spp. The reported proportions of *Leuconostoc* spp. in LAB communities found in artisanal cheeses typically vary between 1 % and 10 % (Campos et al. 2011; Fontana et al. 2010; Menendez et al. 2001; Samelis et al. 2010). Nieto-Arribas et al. (2010) characterized technical properties of 27 *Leuconostoc* isolates from Manchego cheese in order to test their potential as dairy starter cultures. Majority of the isolates belonged to *L. mesenteroides*, although *W. paramesenteroides* and *Leuconostoc lactis* were also found. All isolates grew at high concentrations of NaCl (4.0–4.5 %). They had poor acidifying capacity, no lipolytic activity, and poor capacity to produce diacetyl from citrate. Several isolates showed proteolytic activity. Most of the isolates were considered unsuitable as starter cultures because they grew poorly at pH 4.3.

Weissellas are rarely isolated from cheeses. *W. thailandensis* was a minor part of the halotolerant lactic acid bacteria community in two types of Mexican cheeses that contained 5–6 % of NaCl (Morales et al. 2011). *W. paramesenteroides* was found to be the dominant species of LAB in "dadih," a traditional fermented milk in Indonesia (Hosono et al. 1989). Zakaria et al. (1998) reported *W. paramesenteroides* as one of three predominating LAB species in dadih with different

strains of *W. paramesenteroides* having different influences on its viscosity and curd syneresis.

Kefir is milk drink fermented with kefir grains that consist of bacteria and yeasts. *L. mesenteroides* has been reported to be part of the predominating microbiota in kefir strains together with lactobacilli and yeasts (Hsieh et al. 2012; Kowalczyk et al. 2011; Lin et al. 1999). The use of *L. mesenteroides* in formulated starter cultures for kefir production has also been reported (Duitschaever et al. 1987; Marshall and Cole 1985).

It is known that leuconostocs play a minor role in most traditional milk fermentations. Beukes et al. (2001) collected 15 samples of conventionally fermented milk from households in South Africa and Namibia and found that genera *Leuconostoc*, *Lactococcus*, and *Lactobacillus* predominated the microbial communities. Of the leuconostoc isolates, 83 % were identified as *L. mesenteroides* subsp. *dextranicum*. *L. citreum* was a minor group. In traditional Chinese yak milk products investigated by Bao et al. (2012), *L. mesenteroides* subsp. *mesenteroides* predominated. Yu et al. (2011) identified LAB isolated from several traditional fermented dairy products in Mongolia. Of the 668 isolates, 43 (6.4 %) were identified as *Leuconostoc lactis* or *L. mesenteroides*.

Foods and Beverages of Plant Origin

L. mesenteroides subsp. *mesenteroides* plays an important role in the fermentation of vegetables such as sauerkraut and cucumbers. Although not the dominant species on cabbage at the time of shredding, *L. mesenteroides* subsp. *mesenteroides* initiates the fermentation of sauerkraut and is then succeeded by the more acid-tolerant lactobacilli (Pederson 1930; Stamer 1975). The same microbial succession was observed during fermentation of cucumbers or other pickles as well as olives (Vaughn 1985). Kimchi, a traditional Korean food, is produced by the lactic fermentation of vegetables such as Chinese cabbage, radishes, and cucumbers. Like in sauerkraut fermentation, *Leuconostocs* such as *L. citreum*, *L. gelidum*, *L. kimchii*, and *L. mesenteroides* dominate the early stages of fermentation, followed by lactobacilli (Choi et al. 2003; Kim et al. 2000a, b; Lee et al. 1997), while some *Weissella*-like strains were reported for the midstage of fermentation (Choi et al. 2003).

The sequence of LAB in vegetable fermentations is mainly dependent upon the initial load, growth rates, and salt and acid tolerances (Daeschel et al. 1987). Leuconostocs are apparently better adapted to plant materials and initiate growth more rapidly than most of the other LAB. Some leuconostocs, e.g., *L. mesenteroides* subsp. *mesenteroides*, *L. citreum*, *L. gelidum*, and *L. kimchii*, may be favored by their ability to utilize a wide selection of plant carbohydrates, such as L-arabinose, D-xylose, and sucrose (*Table 18.1*). Furthermore, vegetables contain citrate and fructose, which can be utilized by leuconostocs as electron acceptors for faster growth (Zaunmüller et al. 2006). Carbon dioxide produced by leuconostocs replaces the air and creates an anaerobic atmosphere that inhibits aerobic bacteria (Steinkraus 1983).

The concentration of NaCl added to vegetables in the fermentation process affects the composition of bacterial community. *L. mesenteroides* subsp. *mesenteroides* is less salt tolerant than the other LAB involved in vegetable fermentation (Vaughn 1985). In salt stock pickles, the initial salt concentration is two- to threefold higher than that employed in sauerkraut, and *L. mesenteroides* subsp. *mesenteroides* therefore plays a less-active role in pickle fermentations (Stamer 1988).

Another important factor determining the composition of the bacterial community is the fermentation temperature. Kimchi is often fermented at chilled temperatures (−1 °C to 10 °C) which favors psychrotrophic bacteria (Eom et al. 2007), like *L. gasicomitatum* and *L. gelidum*. *W. koreensis* was identified as the species best adapted at kimchi fermentation at −1 °C (Cho et al. 2006).

Although most of the vegetable fermentations are "spontaneous," the inclusion of *Leuconostoc* strains into starter cultures appears beneficial for the fermentation process and for the development of desirable sensory traits. Using a vegetable juice medium (VJM), Gardner et al. (2001) selected LAB strains for mixed starter cultures to be used in lactic acid fermentation of carrot, beet, and cabbage. Compared to spontaneous fermentation, the inoculation of the vegetables with selected mixed starter cultures accelerated acidification and produced a more stable product. Starter cultures consisting of psychrotrophic *L. mesenteroides* have been successfully applied to accelerate the fermentation of kimchi at +4 °C (Jung et al. 2012d). According to Eom et al. (2007), *L. mesenteroides* and *L. citreum* starter cultures can be used to enhance the production of prebiotic oligosaccharides in kimchi-like foods fermented at low temperatures.

L. mesenteroides and *L. citreum* may be part of predominating LAB community in artisanal wheat sourdough (Corsetti et al. 2001; Robert et al. 2009) and distinctively influences the bread taste (Lönner and Prove-Akesson, 1989). *W. cibaria* and *W. confusa* are also found, although at lesser proportions (Minervini et al. 2012; Robert et al. 2009). Several leuconostocs and weissellas have been introduced to wheat sourdough for the production of exopolysaccharides from sucrose. This is considered as a means to improve the shelf life, volume, and nutritional value of bread without additives. *W. cibaria* and *W. confusa* strains are potential starter cultures for wheat and sorghum sourdoughs due to their high capacity for the production and exopolysaccharides without strong acidification (Galle et al. 2010; Katina et al. 2009).

L. mesenteroides subsp. *mesenteroides* is also predominant and responsible for initiating the fermentation of many traditional lactic acid-fermented foods in the tropics. High numbers of *L. mesenteroides* subsp. *mesenteroides* were isolated from starchy products like cassava (Okafor 1977) or kocho, an African acidic fermented product from false banana (*Ensete ventricosum*; Gashe 1987). Strains of *L. mesenteroides* subsp. *mesenteroides* have been found to produce a highly active linamarase, which hydrolyzes the cyanogenic glucoside linamarin present in cassava (Okafor and Ejiofor 1985). Gueguen et al. (1997) purified and characterized an intracellular β-glucosidase from a strain of *L. mesenteroides* isolated from cassava. When grown on an

arbutin-containing medium, it was found to produce an intracellular β-glucosidase. Its cyanogenic activity was suggested to be of potential interest in cassava detoxification, by hydrolyzing the cyanogenic glucosides present in cassava pulp. *W. confusa* was identified as one of the LAB predominating in highly complex microbial communities in Lafun, an African traditional cassava food (Padonou et al. 2009).

Hancioglu and Karapinar (1997) studied the microflora of Boza, a traditional fermented Turkish beverage, prepared by yeast and lactic acid fermentation of cooked maize, wheat, and rice flours. Among the 77 LAB strains isolated during the fermentation, *W. paramesenteroides* (25.6 %), *L. mesenteroides* subsp. *mesenteroides* (18.6 %), *W. confusa* (7.8 %), *L. mesenteroides* subsp. *dextranicum* (7.3 %), and *O. oeni* (3.7 %) were found. *L. mesenteroides* and *Fructobacillus durionis* were part of a complex microbial community in palm wine made of *Borassus akeassii* (Ouoba et al. 2012). Palm wine was fermented at 21–30 °C and had pH of 3.5–4.1 and ethanol content of 0.3–2.7 %. *L. palmae* was originally isolated from palm wine by Ehrmann et al. (2009).

L. mesenteroides subsp. *mesenteroides* is also involved in the fermentation of seeds of the African oil bean tree (Antai and Ibrahim 1986) and of cocoa (Ostovar and Keeney 1973; Passos et al. 1984). Lefeber et al. (2011) tested metabolic activities of various cocoa-specific *Lactobacillus*, *Leuconostoc*, *Weissella*, and *Fructobacillus* strains in cocoa pulp simulation medium and concluded that citric acid converting, mannitol-producing, heterofermentative, and/or fructose-loving LAB strains are particularly adapted to cocoa pulp matrix. Of the investigated strains, those belonging to *Lactobacillus fermentum* were considered to be the most suitable for the process. Illeghems et al (2012) considered *Leuconostoc mesenteroides* to be only an opportunistic member of the fermentation process wherein a succession of microbial activities of yeasts, LAB, and acetic acid bacteria takes place. Several *Fructobacillus* species have been commonly seen in spontaneous cocoa bean fermentation carried out in different countries (Ecuador, Brazil and Ghana) (Camu et al. 2007; Papalexandratou et al. 2011a, b), suggesting that they play certain key roles for the fermentation. Possible roles might be fructose fermentation and oxygen consumption (Papalexandratou et al. 2011a, b).

L. mesenteroides subsp. *mesenteroides* is also involved in the submerged fermentation of coffee berries, practiced in some highland regions, and by which the oligosaccharide concentration decreases and monosaccharides increase, with a concomitant improvement in coffee quality (Frank and Dela Cruz 1964; Jones and Jones 1984; Müller 1996). Avallone et al. (2001) found that LAB, predominated by *L. mesenteroides*, and yeasts were the microbes mainly responsible for the coffee fermentation. *Leuconostoc holzapfelii* was originally isolated from Ethiopian coffee fermentation (De Bruyne et al. 2007).

Some leuconostocs, lactobacilli, and pediococci are associated with the early stages of fermenting grape must (juice). *Oenococcus oeni*, however, has been reported as the most important and desirable species among the LAB involved in winemaking thanks to its key role in the secondary fermentation of wine, also referred to as the "malolactic fermentation" (MLF). By their high resistance to SO_2 and ethanol, *O. oeni* may be present in relatively high numbers at the end of the alcoholic fermentation. At this stage, they play the major role in the production of microbiologically stable wines by converting L-malic acid to L(+)-lactic acid and CO_2, decreasing wine acidity by 0.1–0.3 units (Davis et al. 1985; Wibowo et al. 1985). This deacidification is particularly desirable for high-acid wine produced in cool-climate regions (Liu 2002). *Lactobacillus* spp. and *Pediococcus* spp. found in wine can also conduct MLF, but, however, these organisms sometimes cause spoilage problems by production of several undesirable volatile compounds (Bartowsky 2009). Some strains of *O. oeni* are also unsuitable for the MLF. Edwards et al. (1998) identified two *O. oeni* strains that were associated with sluggish and/or stuck fermentations and that were found to slow down some alcoholic fermentations. Better control over the MLF can be achieved by inoculating wines with a selected *O. oeni* strain (Nielsen et al. 1996; Rodríguez-Nogales et al. 2012) commercially available in the major wine-growing areas of industrialized countries.

Besides the MLF, citrate metabolism by *O. oeni* is also regarded as important for quality of wine because of the large quantity of citrate in grape juice. Citrate is generally transformed to lactate, acetate, diacetyl, acetoin, and 2,3-butanediol. These chemicals have an impact on quality of wine both positively and negatively (Bartowsky and Borneman 2011).

In addition to wine, MLF by *O. oeni* is important in fermentation of apple cider. Herrero et al. (2001) used *O. oeni* immobilized in alginate beads for controlled malolactic fermentation of cider. The rates of malic acid consumption were similar to conventional fermentation, but a lower acetic acid content and higher concentration of alcohols were detected with immobilized cells. These features were considered to have beneficial effects on the sensory properties of cider (Herrero et al. 2001). Nedovic et al. (2000) succeeded in improving cider quality and to accelerate the process by continuous fermentation with coimmobilized yeast and *O. oeni* cells.

Dextran Production

Dextran is a glucose polymer that has many applications in medicine, separation technology, and biotechnology. The ability of *L. mesenteroides* subsp. *mesenteroides* to produce dextrans from sucrose has been exploited for the production of commercially valuable dextran on an industrial scale. In addition to dextran, leuconostocs are able to produce different types of glucose polymers (glucans) such as alternans and levans from sucrose (Cote and Ahlgren 1995). Glucans are synthesized from sucrose by large extracellular glucosyltransferase enzymes, commonly named glucansucrases. Glucosidic bond synthesis occurs without the mediation of nucleotide-activated sugars and cofactors are not necessary (Monchois et al. 1999). Glucansucrases differ in their ability to synthesize glucans with different types of glucosidic linkages (Kralj et al. 2004).

Dextransucrase is economically the most important glucansucrase. It is mainly produced by *L. mesenteroides* subsp. *mesenteroides*. To develop strategies for improved dextransucrase production, Dols et al. (1997) studied dextran production in relation to the growth and energetics of *L. mesenteroides* NRRL B-1299 during metabolism of various sugars. For sucrose-grown cultures, they found that a large fraction of sucrose is converted outside the cell by dextransucrase into dextran and fructose without supporting growth. The fraction entering the cell is phosphorylated by an inducible sucrose phosphorylase and converted to glucose-6-phosphate (G-6-P) by a constitutive phosphoglucomutase and to heterofermentative metabolites (lactate, acetate, and ethanol). Sucrose was found to support a higher growth rate than the monosaccharides.

In the presence of efficient monomer acceptors, like maltose or isomaltose, dextransucrase catalyzes the synthesis of low molecular weight oligosaccharides instead of high molecular weight dextran (Monchois et al. 1999). Some gluco-oligosaccharides have prebiotic properties, meaning that their industrial production is of interest. The structure and chain length of oligosaccharides can be tailored by changing the concentrations of sucrose and acceptor carbohydrate in the medium (Lee et al. 2008).

Maina et al. (2008) studied the production of gluco-oligosaccharides and linear dextran by *W. confusa* E392 and *L. citreum* E497. The gluco-oligosaccharides were characterized by α-(1→2) linked branches that are associated with probiotic properties. In addition, *W. confusa* E392 was found to be a good alternative to widely used *L. mesenteroides* B-512F in the production of linear dextran. Interestingly, dextransucrases of *Weissella* form a distinct phylogenetic group within glucansucrases of other lactic acid bacteria (Amari et al. 2012a).

References

Albano H, van Reenen CA, Todorov SD, Cruz D, Fraga L, Hogg T, Dicks LMT, Teixeira P (2009) Phenotypic and genetic heterogeneity of lactic acid bacteria isolated from "Alheira", a traditional fermented sausage produced in Portugal. Meat Sci 82:389–398

Amari M, Arango LFG, Gabriel V, Robert H, Morel S, Moulis C, Gabriel B, Remaud-Siméon M, Fontagné-Faucher C (2012a) Characterization of a novel dextransucrase from *Weissella confusa* isolated from sourdough. Appl Microbiol Biotechnol 97(12):5413–5422

Amari M, Laguerre S, Vuillemin M, Robert H, Loux V, Klopp C, Morel S, Gabriel B, Remaud-Siméon M, Gabriel V, Moulis C, Fontagné-Faucher C (2012b) Genome sequence of *Weissella confusa* LBAE C39-2, isolated from a wheat sourdough. J Bacteriol 194:1608–1609

Amerine MA, Berg HW, Kunkee RE, Ough CS, Singleton VL, Webb AD (1980) The technology of wine making, 4th edn. AVI, Westport

Ampe F, Ben Omar N, Moizan C, Wacher C, Guyot J-P (1999) Polyphasic study of the spatial distribution of microorganisms in Mexican pozol, a fermented maize dough, demonstrates the need for cultivation-independent methods to investigate traditional fermentations. Appl Environ Microbiol 65:5464–5473

Antai SP, Ibrahim MH (1986) Microorganisms associated with African locust bean (*Parkia-Filicoidea*) fermentation for "dawadawa" production. J Appl Bacteriol 6l:145–148

Antunes A, Rainey FA, Nobre MF, Schumann P, Ferreira AM, Ramos A, Santos H, da Costa MS (2002) *Leuconostoc ficulneum* sp. nov., a novel lactic acid bacterium isolated from a ripe fig, and reclassification of *Lactobacillus fructosus* as *Leuconostoc fructosum* comb. nov. Int J Syst Evol Microbiol 52:647–655

Arahal DR, Sanchez E, Macian MC, Garay E (2008) Value of *recN* sequences for species identification and as a phylogenetic marker within the family "*Leuconostocaceae*". Int Microbiol 11:33–39

Auch AF, von Jan M, Klenk H-P, Göker M (2010) Digital DNA-DNA hybridization for microbial species delineation by means of genome-to-genome sequence comparison. Stand Genomic Sci 2:117–134

Avallone S, Guyot B, Brillouet JM, Olguin E, Guiraud JP (2001) Microbiological and biochemical study of coffee fermentation. Curr Microbiol 42:252–256

Aymerich T, Martín B, Garriga M, Vidal-Carou MC, Bover-Cid S, Hugas M (2006) Safety properties and molecular strain typing of lactic acid bacteria from slightly fermented sausages. J Appl Microbiol 100:40–49

Aznar R, Chenoll E (2006) Intraspecific diversity of *Lactobacillus curvatus*, *Lactobacillus plantarum*, *Lactobacillus sakei*, and *Leuconostoc mesenteroides* associated with vacuum-packed meat product spoilage analyzed by randomly amplified polymorphic DNA PCR. J Food Prot 69:2403–2410

Babic I, Markov K, Kovacevic D, Trontel A, Slavica A, Dugum J, Cvek D, Svetec IK, Posavec S, Frece J (2011) Identification and characterization of potential autochthonous starter cultures from a Croatian "brand" product "Slavonski kulen". Meat Sci 88:517–524

Bao Q, Liu W, Yu J, Wang W, Qing M, Chen X, Wang F, Zhang J, Zhang W, Qiao J, Sun T, Zhang H (2012) Isolation and identification of cultivable lactic acid bacteria in traditional yak milk products of Gansu Province in China. J Gen Appl Microbiol 58:95–105

Bartowsky EJ (2009) Bacterial spoilage of wine and approaches to minimize it. Lett Appl Microbiol 48:149–156

Bartowsky EJ, Borneman AR (2011) Genomic variations of *Oenococcus oeni* strains and the potential to impact on malolactic fermentation and aroma compounds in wine. Appl Microbiol Biotechnol 92:441–447

Bartowsky EJ, McCarthy JM, Henschke P (2003) Differentiation of Australian wine isolates of *Oenococcus oeni* using random amplified polymorphic DNA (RAPD). Aust J Grape Wine Res 9:122–126

Ben Belgacem Z, Dousset X, Prévost H, Manai M (2009) Polyphasic taxonomic studies of lactic acid bacteria associated with Tunisian fermented meat based on the heterogeneity of the 16S-23S rRNA gene intergenic spacer region. Arch Microbiol 191:711–720

Benito MJ, Martín A, Aranda E, Pérez-Nevado F, Ruiz-Moyano S, Córdoba MG (2007) Characterization and selection of autochthonous lactic acid bacteria isolated from traditional Iberian dry-fermented salchichón and chorizo sausages. J Food Sci 72:M193–M201

Benomar N, Abriouel H, Lee H, Cho G-S, Huch M, Pulido RP, Holzapfel WH, Gálvez A, Franz CMAP (2011) Genome sequence of *Weissella thailandensis* fsh4-2. J Bacteriol 193:5868

Beukes EM, Bester BH, Mostert JF (2001) The microbiology of South African traditional fermented milks. Int J Food Microbiol 63:189–197

Bilhere E, Lucas PM, Claisse O, Lonvaud-Funel A (2009) Multilocus sequence typing of *Oenococcus oeni*: detection of two subpopulations shaped by intergenic recombination. Appl Environ Microbiol 75:1291–1300

Björkroth J, Holzapfel WH (2006) Genera *Leuconostoc*, *Oenococcus* and *Weissella*. In: Dworkin M, Falkow S, Rosenberg E, Schleifer K-H, Stackebrandt E (eds) The prokaryotes: a handbook on the biology of bacteria: *Firmicutes*, *Cyanobacteria*, vol 4, 3rd edn. Springer, Dordrecht/Heidelberg/London/New York, pp 267–319

Björkroth KJ, Vandamme P, Korkeala HJ (1998) Identification and characterization of *Leuconostoc carnosum*, associated with production and spoilage of vacuum-packaged, sliced, cooked ham. Appl Environ Microbiol 64:3313–3319

Björkroth J, Geisen R, Schillinger U, Weiss N, De Vos P, Holzapfel WH, Korkeala HJ, Vandamme P (2000) Characterization of *Leuconostoc gasicomitatum* sp. nov. associated with spoiled raw tomato-marinated broiler meat strips packaged under modified atmosphere. Appl Environ Microbiol 66:3764–3772

Björkroth J, Schillinger U, Geisen R, Weiss N, Holzapfel WH, Korkeala HJ, Vandamme P (2002) Taxonomic study of *Weissella confusa* and description of *Weissella cibaria* sp. nov., a novel species detected in food and clinical samples. Int J Syst Evol Microbiol 52:141–148

Björkroth J, Dicks LMT, Holzapfel WH (2009) Genus III. *Weissella* Collins, Samelis, Metaxopoulos and Wallbanks 1994, 370^{VP} (Effective publication: Collins, Samelis Metaxopoulos and Wallbanks 1993, 597). In: De Vos P, Garrity GM, Jones D, Krieg NR, Ludwig W, Rainey FA, Schleifer KH, Whitman WB (eds) Bergey's manual of systematic bacteriology (The Firmicutes), vol 3, 2nd edn. Springer, Dordrecht/Heidelberg/London/New York, pp 643–653

Boissy R, Ahmed A, Janto B, Earl J, Hall BG, Hogg JS, Pusch GD, Hiller LN, Powell E, Hayes J, Yu S, Kathju S, Stoodley P, Post JC, Ehrlich GD, Hu FZ (2011) Comparative supragenomic analyses among the pathogens *Staphylococcus aureus*, *Streptococcus pneumoniae*, and *Haemophilus influenzae* using a modification of the finite supragenome model. BMC Genomics 12:187

Bonnin-Jusserand M, Grandvalet C, David V, Alexandre H (2011) Molecular cloning, heterologous expression, and characterization of ornithine decarboxylase from *Oenococcus oeni*. J Food Prot 74:1309–1314

Bonomo MG, Ricciardi A, Zotta T, Parente E, Salzano G (2008) Molecular and technological characterization of lactic acid bacteria from traditional fermented sausages of Basilicata region (Southern Italy). Meat Sci 80:1238–1248

Borneman AR, Bartowsky EJ, McCarthy J, Chambers PJ (2010) Genotypic diversity in *Oenococcus oeni* by high-density microarray comparative genome hybridization and whole genome sequencing. Appl Microbiol Biotechnol 862:681–691

Borneman AR, McCarthy JM, Chambers PJ, Bartowsky EJ (2012a) Functional divergence in the genus *Oenococcus* as predicted by genome sequencing of the newly-described species, *Oenococcus kitaharae*. PLoS One 7:e29626

Borneman AR, McCarthy JM, Chambers PJ, Bartowsky EJ (2012b) Comparative analysis of the *Oenococcus oeni* pan genome reveals genetic diversity in industrially-relevant pathways. BMC Genomics 13:373

Bounaix MS, Gabriel V, Robert H, Morel S, Remaud-Siméon M, Gabriel B, Fontagné-Faucher C (2010a) Characterization of glucan-producing *Leuconostoc* strains isolated from sourdough. Int J Food Microbiol 144:1–9

Bounaix MS, Robert H, Gabriel V, Morel S, Remaud-Siméon M, Gabriel B, Fontagné-Faucher C (2010b) Characterization of dextran-producing *Weissella* strains isolated from sourdoughs and evidence of constitutive dextransucrase expression. FEMS Microbiol Lett 311:18–26

Bover-Cid S, Holzapfel WH (1999) Improved screening procedure for biogenic amine production by lactic acid bacteria. Int J Food Microbiol 53:33–41

Bridier J, Claisse O, Coton M, Coton E, Lonvaud-Funel A (2010) Evidence of distinct populations and specific subpopulations within the species *Oenococcus oeni*. Appl Environ Microbiol 76:7754–7764

Brito L, Paveia H (1999) Presence and analysis of large plasmids in *Oenococcus oeni*. Plasmid 413:260–267

Broadbent JR, Neeno-Eckwall EC, Stahl B, Tandee K, Cai H, Morovic W, Horvath P, Heidenreich J, Perna NT, Barrangou R, Steele JL (2012) Analysis of the *Lactobacillus casei* supragenome and its influence in species evolution and lifestyle adaptation. BMC Genomics 131:533

Brooijmans R, Smit B, Santos F, van Riel J, de Vos WM, Hugenholtz J (2009) Heme and menaquinone induced electron transport in lactic acid bacteria. Microb Cell Fact 8:28

Buu-Hoi A, Branger C, Acar JF (1985) Vancomycin-resistant streptococci or *Leuconostoc* sp. Antimicrob Agents Chemother 28:458–460

Campos G, Robles L, Alonso R, Nuñez M, Picon A (2011) Microbial dynamics during the ripening of a mixed cow and goat milk cheese manufactured using frozen goat milk curd. J Dairy Sci 94:4766–4776

Camu N, De Winter T, Verbrugghe K, Cleenwerck I, Vandamme P, Takrama JS, Vancanneyt M, De Vuyst L (2007) Dynamics and biodiversity of populations of lactic acid bacteria and acetic acid bacteria involved in spontaneous heap fermentation of cocoa beans in Ghana. Appl Environ Microbiol 73:1809–1824

Cappello M, Stefani D, Grieco F, Logrieco A, Zapparoli G (2008) Genotyping by amplified fragment length polymorphism and malate metabolism performances of indigenous *Oenococcus oeni* strains isolated from Primitivo wine. Int J Food Microbiol 127:241–245

Cappello M, Zapparoli G, Stefani D, Logrieco A (2010) Molecular and biochemical diversity of *Oenococcus oeni* strains isolated during spontaneous malolactic fermentation of Malvasia Nera wine. Syst Appl Microbiol 33:461–467

Carreté R, Vidal MT, Bordons A, Constantí M (2002) Inhibitory effect of sulfur dioxide and other stress compounds in wine on the ATPase activity of *Oenococcus oeni*. FEMS Microbiol Lett 211:155–159

Chambel L, Chelo IM, Zé-Zé L, Pedro LG, Santos MA, Tenreiro R (2006) *Leuconostoc pseudoficulneum* sp. nov., isolated from a ripe fig. Int J Syst Evol Microbiol 56:1375–1381

Chelo IM, Ze-Ze L, Tenreiro R (2007) Congruence of evolutionary relationships inside the *Leuconostoc-Oenococcus-Weissella* clade assessed by phylogenetic analysis of the 16S rRNA gene, dnaA, gyrB, rpoC and dnaK. Int J Syst Evol Microbiol 57:276–286

Chelo IM, Zé-Zé L, Tenreiro R (2010) Genome diversity in the genera *Fructobacillus*, *Leuconostoc* and *Weissella* determined by physical and genetic mapping. Microbiology 156:420–430

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

Chenoll E, Macián MC, Aznar R (2003) Identification of *Carnobacterium*, *Lactobacillus*, *Leuconostoc* and *Pediococcus* by rDNA-based techniques. Syst Appli Microbiol 26(4):546–556

Chenoll E, Macián MC, Elizaquível P, Aznar R (2007) Lactic acid bacteria associated with vacuum-packed cooked meat product spoilage: population analysis by rDNA-based methods. J Appl Microbiol 102(2):498–508. doi:10.1111/j.1365-2672.2006.03081.x

Cho J, Lee D, Yang C, Jeon J, Kim J, Han H (2006) Microbial population dynamics of kimchi, a fermented cabbage product. FEMS Microbiol Lett 257:262–267

Choi H-J, Cheigh C-I, Kim S-B, Lee J-C, Lee D-W, Choi S-W, Park J-M, Pyun Y-R (2002) *Weissella kimchii* sp. nov., a novel lactic acid bacterium isolated from kimchi. Int J Syst Appl Microbiol 52:507–511

Choi I-K, Jung S-H, Kim B-J, Park S-Y, Kim J, Han H-U (2003) Novel *Leuconostoc citreum* starter culture system for fermentation of kimchi, a fermented cabbage product. Antonie Van Leeuwenhoek 84(4):247–253

Cibik R, Lepage E, Talliez P (2000) Molecular diversity of *Leuconostoc* mesenteroides and *Leuconostoc* citreum isolated from traditional French cheeses as revealed by RAPD fingerprinting, 16S rDNA sequencing and 16S rDNA fragment amplification. Syst Appl Microbiol 23:267–278

Cogan TM, Barbosa M, Beuvier E, Bianchi-Salvadori B, Cocconcelli PS, Fernandes I, Gomez J, Gomez R, Kalantzopoulos G, Ledda A, Medina M, Rea MC, Rodriguez E (1997) Characterization of the lactic acid bacteria in artisanal dairy products. J Dairy Res 64:409–421

Collins MD, Samelis J, Metaxopoulus J, Wallbanks S (1993) Taxonomic studies on some leuconostoc-like organisms from fermented sausages: Description of a new genus *Weissella* for the *Leuconostoc paramesenteroides* group of species. J Appl Bacteriol 75:595–603

Condon S (1987) Responses of lactic acid bacteria to oxygen. FEMS Microbiol Lett 46:269–280

Corsetti A, Lavermicocca P, Morea M, Baruzzi F, Tosti N, Gobbetti M (2001) Phenotypic and molecular identification and clustering of lactic acid bacteria and yeasts from wheat (species *Triticum durum* and *Triticum aestivum*) sourdoughs of Southern Italy. Int J Food Microbiol 64:95–104

Cote GL, Ahlgren JA (1995) Microbial polysaccharides. In: Kroschwitz JI, Howe-Grant M (eds) Kirk-Othmer encyclopedia of chemical technology, vol 16, 4th edn. Wiley, New York, pp 578–611

Daeschel MA, Andersson RE, Fleming HP (1987) Microbial ecology of fermenting plant materials. FEMS Microbiol Rev 46:357–367

Danilovic B, Jokovic N, Petrovic L, Veljovic K, Tolinacki M, Savic D (2011) The characterisation of lactic acid bacteria during the fermentation of an artisan Serbian sausage (Petrovská Klobása). Meat Sci 88:668–674

Davis G, Silveira NFA, Fleet GH (1985) Occurrence and properties of bacteriophages of *Leuconostoc oenos* in Australian wines. Appl Environ Microbiol 50:872–876

De Bruyne K, Schillinger U, Caroline L, Boehringer B, Cleenwerck I, Vancanneyt M, De Vuyst L, Franz CMAP, Vandamme P (2007) *Leuconostoc holzapfelii* sp. nov., isolated from Ethiopian coffee fermentation and assessment of sequence analysis of housekeeping genes for delineation of *Leuconostoc* species. Int J Syst Evol Microbiol 57:2952–2959

De Bruyne K, Camu N, Lefebvre K, De Vuyst L, Vandamme P (2008) *Weissella ghanensis* sp. nov., isolated from a Ghanaian cocoa fermentation. Int J Syst Evol Microbiol 58:2721–2725

De Bruyne K, Camu N, De Vuyst L, Vandamme P (2010) *Weissella fabaria* sp. nov., from a Ghanaian cocoa fermentation. Int J Syst Evol Microbiol 60:1999–2005

De Bruyne K, Slabbinck B, Waegeman W, Vauterin P, De Baets B, Vandamme P (2011) Bacterial species identification from MALDI-TOF mass spectra through data analysis and machine learning. Syst Appl Microbiol 34(1):20–29

de Las Rivas B, Marcobal A, Munoz R (2004) Allelic diversity and population structure in *Oenococcus oeni* as determined from sequence analysis of housekeeping genes. Appl Environ Microbiol 70:7210–7219

de Llano DG, Cuesta P, Rodríguez A (1998) Biogenic amine production by wild lactococcal and leuconostoc strains. Lett Appl Microbiol 26:270–274

De Man JC, Rogosa M, Sharpe EM (1960) A medium for the cultivation of lactobacilli. J Appl Microbiol 23:130–135

De Vuyst L, Schrijvers V, Paramithiotis S, Hoste B, Vancanneyt M, Swings J, Kalantzopoulos G, Tsakalidou E, Messens W (2002) The biodiversity of lactic acid bacteria in Greek traditional wheat sourdoughs is reflected in both composition and metabolite formation. Appl Environ Microbiol 68:6059–6069

Dicks LMT, Holzapfel WH (2009) Genus II. *Oenococcus* Dicks, Dellaglio and Collins 1995a, 396^{VP}. In: De Vos P, Garrity GM, Jones D, Krieg NR, Ludwig W, Rainey FA, Schleifer KH, Whitman WB (eds) Bergey's manual of systematic bacteriology (The Firmicutes), vol 3, 2nd edn. Springer, Dordrecht/Heidelberg/London/New York, pp 635–642

Dicks LM, van Vuuren HJ, Dellaglio F (1990) Taxonomy of *Leuconostoc* species, particularly *Leuconostoc oenos*, as revealed by numerical analysis of total soluble cell protein patterns, DNA base compositions, and DNA-DNA hybridizations. Int J Syst Bacteriol 40:83–91

Dicks LMT, Dellaglio F, Collins MD (1995) Proposal to reclassify *Leuconostoc oenos* as *Oenococcus oeni* corrig. gen. nov., comb. nov. Int J Syst Bacteriol 45:395–397

Diez AM, Bjorkroth J, Jaime I, 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

Dols M, Chraibi W, Remaud-Simeon M, Lindley ND, Monsan PF (1997) Growth and energetics of *Leuconostoc mesenteroides* NRRL B-1299 during metabolism of various sugars and their consequences for dextransucrase production. Appl Environ Microbiol 63:2159–2165

Duitschaever CL, Kemp N, Emmons E (1987) Pure culture formulation and procedure for the production of kefir. Milchwissenschaft 42:80–82

Edwards RA, Dainty RH, Hibbard CM, Ramantanis SV (1987) Amines in fresh beef of normal pH and the role of bacteria in changes in concentration observed during storage in vacuum packs at chill temperatures. J Appl Bacteriol 63:427–434

Edwards CG, Haag KM, Collins MD (1998) Identification and characterization of two lactic acid bacteria associated with sluggish/stuck fermentations. Am J Enol Viticult 49:445–448

Ehrmann MA, Freiding S, Vogel RF (2009) *Leuconostoc palmae* sp. nov., a novel lactic acid bacterium isolated from palm wine. Int J Syst Evol Microbiol 59:943–947

Elisha BG, Courvalin P (1995) Analysis of genes encoding D-alanine: D-alanine ligase-related enzymes in *Leuconostoc mesenteroides* and *Lactobacillus* spp. Gene 152:79–83

Endo A, Okada S (2006) *Oenococcus kitaharae* sp. nov., a non-acidophilic and non-malolactic-fermenting oenococcus isolated from a composting distilled shochu residue. Int J Syst Evol Microbiol 56:2345–2348

Endo A, Okada S (2008) Reclassification of the genus *Leuconostoc*, and proposals of *Fructobacillus fructosus* gen. nov., comb. nov., *Fructobacillus durionis* comb. nov., *Fructobacillus ficulneus* comb. nov. and *Fructobacillus pseudoficulneus* comb. nov. Int J Syst Evol Microbiol 58:2195–2205

Endo A, Futagawa-Endo Y, Dicks LMT (2009) Isolation and characterization of fructophilic lactic acid bacteria from fructose-rich niches. Syst Appl Microbiol 32:593–600

Endo A, Irisawa T, Futagawa-Endo Y, Sonomoto K, Itoh K, Takano K, Okada S, Dicks LMT (2011) *Fructobacillus tropaeoli* sp. nov., a novel fructophilic lactic acid bacterium isolated from a flower. Int J Syst Evol Microbiol 61:898–902

Ennahar S, 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

Eom H-J, Seo DM, Han NS (2007) Selection of psychrotrophic *Leuconostoc* spp. producing highly active dextransucrase from lactate fermented vegetables. Int J Food Microbiol 117:61–67

Evans JB, Niven CF Jr (1951) Nutrition of the heterofermentative lactobacilli that cause greening of cured meat products. J Bacteriol 62:599–603

Farrow JAE, Facklam RR, Collins MD (1989) Nucleic acid homologies of some vancomycin-resistant leuconostocs and description of *Leuconostoc citreum* sp. nov. and *Leuconostoc pseudomesenteroides*. Int J Syst Bacteriol 39:279–283

Flaherty JD, Levett PN, Dewhirst FE, Troe TE, Warren JR, Johnson S (2003) Fatal case of endocarditis due to *Weissella confusa*. J Clin Microbiol 41:2237–2239

Fontana C, Cappa F, Rebecchi A, Cocconcelli PS (2010) Surface microbiota analysis of Taleggio, Gorgonzola, Casera, Scimudin and Formaggio di Fossa Italian cheeses. Int J Food Microbiol 138:205–211

Frank HA, Dela Cruz AS (1964) Role of incidental microflora in natural decomposition of mucilage layer in Kona coffee. J Food Sci 29:850–853

Galle S, Schwab C, Arendt E, Gänzle M (2010) Exopolysaccharide-forming *Weissella* strains as starter cultures for sorghum and wheat sourdoughs. J Agric Food Chem 58:5834–5841

Garcia-Moruno E, Muñoz R (2012) Does *Oenococcus oeni* produce histamine? Int J Food Microbiol 157:121–129

Gardini F, Zaccarelli A, Belletti N, Faustini F, Cavazza A, Martuscelli M, Mastrocola D, Suzzi G (2005) Factors influencing biogenic amine production by a strain of *Oenococcus oeni* in a model system. Food Control 16:609–616

Gardner NJ, Savard T, Obermeier P, Caldwell G, Champagne CP (2001) Selection and characterisation of mixed starter cultures for lactic acid fermentation of carrot, cabbage, beet and onion vegetable mixtures. Int J Food Microbiol 64:261–275

Garvie EI (1967a) The growth factor and amino acid requirements of species of the genus *Leuconostoc*, including *Leuconostoc paramesenteroides* (sp. nov.) and *Leuconostoc oenos*. J Gen Microbiol 48:439–447

Garvie EI (1967b) *Leuconostoc oenos* sp. nov. J Gen Microbiol 48:431–438

Garvie EI (1975) Some properties of gas forming lactic acid bacteria and their significance in classification. In: Carr JG, Cutting DV, Whiting GC (eds) Lactic acid bacteria in beverages and food. Academic, London

Garvie EI (1976) Hybridization between the deoxyribonucleic acids of some strains of heterofermentative lactic acid bacteria. Int J Syst Bacteriol 26:116–122

Garvie EI (1986) Genus *Leuconostoc* van Tieghem 1878, 198^{AL} emend. mut. char. Hucker and Pederson 1930, 66^{AL}. In: Sneath PHA, Mair NS, Sharpe MS, Holt JG (eds) Bergey's manual of systematic bacteriology. Williams and Wilkins, Baltimore, pp 1071–1075

Garvie EI, Mabbitt LA (1967) Stimulation of the growth of *Leuconostoc oenos* by tomato juice. Arch Mikrobiol 55:398–407

Gashe BA (1987) Kocho fermentation. J Appl Bacteriol 62:473–478

Gu CT, Wang F, Li CY, Liu F, Huo GC (2012) *Leuconostoc mesenteroides* subsp. *suionicum* subsp. nov. Int J Syst Evol Microbiol 62:1548–1551

Gueguen Y, Chemardin P, Labrot P, Arnaud A, Galzy P (1997) Purification and characterization of an intracellular beta-glucosidase from a new strain of *Leuconostoc mesenteroides* isolated from cassava. J Appl Microbiol 82:469–476

Guerini S, Mangani S, Granchi L, Vincenzini M (2002) Biogenic amine production by *Oenococcus oeni*. Curr Microbiol 44:374–378

Hancioglu O, Karapinar M (1997) Microflora of Boza, a traditional fermented Turkish beverage. Int J Food Microbiol 35:271–274

Harlan NP, Kempker RR, Parekh SM, Burd EM, Kuhar DT (2011) *Weissella confusa* bacteremia in a liver transplant patient with hepatic artery thrombosis. Transpl Infect Dis 13:290–293

Hastings JW, Stiles ME, von Holy A (1994) Bacteriocins of leuconostocs isolated from meat. Int J Food Microbiol 24:75–81

He H, Chen Y, Zhang Y, Wei C (2011) Bacteria associated with gut lumen of *Camponotus japonicus* Mayr. Environ Entomol 40:1405–1409

Hemme D, Foucaud-Scheunemann C (2004) *Leuconostoc*, characteristics, use in dairy technology and prospects in functional foods. Int Dairy J 14:467–494

Herrero M, Laca A, Garcia LA, Diaz M (2001) Controlled malolactic fermentation in cider using *Oenococcus oeni* immobilized in alginate beads and comparison with free cell fermentation. Enzyme Microb Technol 28:35–41

Holzapfel W (1998) The Gram-positive bacteria associated with meat and meat products. In: Davies A, Board R (eds) The microbiology of meat and poultry. Blackie Academic and Professional, London, pp 35–74

Holzapfel WH, Kandler O (1969) Zur Taxonomie der Gattung *Lactobacillus* Beijernick. VI.*Lactobacillus coprophilus* subsp. *confusus* nov. subsp., eine neue Unterart der Untergattung *Betabacterium*. Zentbl Bakteriol Parasitenkd Infektionskr Hyg 123:657–666

Holzapfel WH, van Wyk EP (1982) *Lactobacillus kandleri* sp. nov., a new species of the subgenus *Betabacterium* with glycine in the peptidoglycan. Zentbl Bakteriol Parasitenkd Infektionskr Hyg C3:495–502

Holzapfel WH, Björkroth J, Dicks LMT (2009) Genus I. *Leuconostoc* van Tieghem 1878, 198^{AL} emend. mut. char. (Hucker and Pederson 1930), 66^{AL}. In: De Vos P, Garrity GM, Jones D, Krieg NR, Ludwig W, Rainey FA, Schleifer KH, Whitman WB (eds) Bergey's manual of systematic bacteriology (The Firmicutes), vol 3, 2nd edn. Springer, Dordrecht/Heidelberg/London/New York, pp 624–634

Hosono A, Wardojo R, Otani H (1989) Microbial flora in dadih, a traditional fermented milk in Indonesia. Lebensm Wiss Technol 22:20–24

Hsieh H-H, Wang S-Y, Chen T-L, Huang Y-L, Chen M-J (2012) Effects of cow's and goat's milk as fermentation media on the microbial ecology of sugary kefir grains. Int J Food Microbiol 157:73–81

Hucker GJ, Pederson CS (1930) Studies on the Coccoceae XVI. The Genus *Leuconostoc*. N.Y. Agric Exp Sta Bull 167:3–80

Huygens F (1993) Vancomycin binding to cell walls of non-streptococcal vancomycin-resistant bacteria. J Antimicrob Chemother 32:551–558

Illeghems K, De Vuyst L, Papalexandratou Z, Weckx S (2012) Phylogenetic analysis of a spontaneous cocoa bean fermentation metagenome reveals new insights into its bacterial and fungal community diversity. PLoS One 7:e38040

Izquierdo Cañas PM, Gómez Alonso S, Ruiz Pérez P, Seseña Prieto S, García Romero E, Palop Herreros ML (2009) Biogenic amine production by *Oenococcus oeni* isolates from malolactic fermentation of Tempranillo wine. J Food Prot 72:907–910

Jang J, Kim B, Lee J, Kim J, Jeong G, Han H (2002) Identification of *Weissella* species by the genus-specific amplified ribosomal DNA restriction analysis. FEMS Microbiol Lett 212:29–34

Jang J, Kim B, Lee J, Han H (2003) A rapid method for identification of typical *Leuconostoc* species by 16S rDNA PCR-RFLP analysis. J Microbiol Methods 55:295–302

Johansson P, Paulin L, Vihavainen E, Salovuori N, Alatalo ER, Björkroth KJ (2011) Genome sequence of a food spoilage lactic acid bacterium *Leuconostoc gasicomitatum* LMG 18811T in association with specific spoilage reactions. Appl Environ Microbiol 77:4344–4351

Jones KL, Jones SE (1984) Fermentations involved in the production of cocoa, coffee and tea. Prog Ind Microbiol 19:411–456

Jung JY, Lee SH, Jeon CO (2012a) Complete genome sequence of *Leuconostoc carnosum* strain JB16, isolated from kimchi. J Bacteriol 194:6672–6673

Jung JY, Lee SH, Jeon CO (2012b) Complete genome sequence of *Leuconostoc gelidum* strain JB7, isolated from kimchi. J Bacteriol 194:6665

Jung JY, Lee SH, Lee SH, Jeon CO (2012c) Complete genome sequence of *Leuconostoc mesenteroides* subsp. *mesenteroides* strain J18, isolated from kimchi. J Bacteriol 194:730–731

Jung JY, Lee SH, Lee HJ, Seo H-Y, Park W-S, Jeon CO (2012d) Effects of *Leuconostoc mesenteroides* starter cultures on microbial communities and metabolites during kimchi fermentation. Int J Food Microbiol 153:378–387

Kandler O, Abo-Elnaga IG (1966) Zur Taxonomie der Gattung *Lactobacillus* Beijerinck. IV. *L. corynoides* ein Synonym von *L. viridescens*. Zentrbl Bakteriol Parasitenkd Infektionskr Hyg 120:753–759

Kandler O, Schillinger U, Weiss N (1983) *Lactobacillus halotolerans* sp. nov, nom. rev. and *Lactobacillus minor* sp. nov., nom. rev. System Appl Microbiol 4:280–285

Katina K, Maina NH, Juvonen R, Flander L, Johansson L, Virkki L, Tenkanen M, Laitila A (2009) *In situ* production and analysis of *Weissella confusa* dextran in wheat sourdough. Food Microbiol 26:734–743

Kesmen Z, Yetiman AE, Gulluce A, Kacmaz N, Sagdic O, Cetin B, Adiguzel A, Sahin F, Yetim H (2012) Combination of culture-dependent and culture-independent molecular methods for the determination of lactic microbiota in sucuk. Int J Food Microbiol 153:428–435

Kim M, Chun J (2005) Bacterial community structure in Kimchi, a Korean fermented vegetable food, as revealed by 16S rRNA gene analysis. Int J Food Microbiol 103:91–96

Kim J, Chun J, Han H-U (2000a) *Leuconostoc kimchii* sp. nov., a new species from kimchi. Int J Syst Evol Microbiol 50:1915–1919

Kim B-J, Lee H-J, Park S-Y, Kim J, Han H-U (2000b) Identification and characterisation of *Leuconostoc gelidum* isolated from kimchi, a fermented cabbage product. J Microbiol 38:132–135

Kim B, Lee J, Jang J, Kim J, Han H (2003) *Leuconostoc inhae* sp. nov., a lactic acid bacterium isolated from kimchi. Int J Syst Evol Microbiol 53:1123–1126

Kim JF, Jeong H, Lee J-S, Choi S-H, Ha M, Hur C-G, Kim J-S, Lee S, Park H-S, Park Y-H, Oh TK (2008) The complete genome sequence of *Leuconostoc citreum* KM20. J Bacteriol 190:3093–3094

Kim D-W, Choi S-H, Kang A, Nam S-H, Kim RN, Kim A, Kim D-S, Park H-S (2011a) Genome sequence of *Leuconostoc pseudomesenteroides* KCTC 3652. J Bacteriol 193:4299

Kim D-S, Choi S-H, Kim D-W, Kim RN, Nam S-H, Kang A, Kim A, Park H-S (2011b) Genome sequence of *Leuconostoc gelidum* KCTC 3527, isolated from kimchi. J Bacteriol 193:799–800

Kim D-S, Choi S-H, Kim D-W, Nam S-H, Kim RN, Kang A, Kim A, Park H-S (2011c) Genome sequence of *Weissella cibaria* KACC 11862. J Bacteriol 193:797–798

Kiviharju K, Nyyssölä A (2008) Contributions of biotechnology to the production of mannitol. Recent Pat Biotechnol 2:73–78

Koch H, Schmid-Hempel P (2011) Bacterial communities in central European bumblebees: low diversity and high specificity. Microb Ecol 62:121–133

Kodama R (1956) Studies on the nutrition of lactic acid bacteria. Part IV. *Lactobacillus fructosus* nov. sp., a new species of lactic acid bacteria. J Agr Chem Soc Jpn 30:05–708

Konstantinidis KT, Tiedje JM (2005) Towards a genome-based taxonomy for prokaryotes. J Bacteriol 187:6258–6264

Koort J, Coenye T, Santos EM, Molinero C, Jaime I, Rovira J, Vandamme P, Bjorkroth J (2006) Diversity of *Weissella viridescens* strains associated with "Morcilla De Burgos". Int J Food Microbiol 109:164–168

Kowalczyk M, Kolakowski P, Radziwill-Bienkowska JM, Szmytkowska A, Bardowski J (2011) Cascade cell lyses and DNA extraction for identification of genes and microorganisms in kefir grains. J Dairy Res 79:26–32

Kralj S, van Geel-Schutten GH, Dondorff MMG, Kirsanovs S, van der Maarel MJEC, Dijkhuizen L (2004) Glucan synthesis in the genus *Lactobacillus*: isolation and characterization of glucansucrase genes, enzymes and glucan products from six different strains. Microbiology 150:3681–3690

Laguerre S, Amari M, Vuillemin M, Robert H, Loux V, Klopp C, Morel S, Gabriel B, Remaud-Siméon M, Gabriel V, Moulis C, Fontagné-Faucher C (2012) Genome sequences of three *Leuconostoc citreum* strains, LBAE C10, LBAE C11, and LBAE E16, isolated from wheat sourdoughs. J Bacteriol 194:1610–1611

Le Jeune C, Lonvaud-Funel A (1997) Sequence of DNA 16S/23S spacer region of *Leuconostoc oenos* (*Oenococcus oeni*): application to strain differentiation. Res Microbiol 148:79–86

Lee J-S, Chun CO, Hector M, Kim S-B, Kim H-J, Park B-K, Joo Y-J, Lee H-J, Park C-S, Ahn J-S, Park Y-H, Mheen T-L (1997) Identification of *Leuconostoc* strains isolated from kimchi using carbon-source utilisation patterns. J Microbiol 35:10–14

Lee J-S, Lee KC, Ahn J-S, Mheen T-I, Pyun Y-R, Park Y-H (2002) *Weissella koreensis* sp. nov., isolated from kimchi. Int J Syst Evol Microbiol 52:1257–1261

Lee MS, Cho SK, Eom H-J, Kim S-Y, Kim T-J, Han NS (2008) Optimized substrate concentrations for production of long-chain isomaltooligosaccharides using dextransucrase of *Leuconostoc mesenteroides* B-512F. J Microbiol Biotechnol 18:1141–1145

Lee MR, Huang YT, Liao CH, Lai CC, Lee PI, Hsueh PR (2011a) Bacteraemia caused by *Weissella confusa* at a university hospital in Taiwan, 1997–2007. Clin Microbiol Infect 17:1226–1231

Lee SH, Jung JY, Lee SH, Jeon CO (2011b) Complete genome sequence of *Weissella koreensis* KACC 15510, isolated from kimchi. J Bacteriol 193:5534

Lee SH, Jung JY, Lee SH, Jeon CO (2011c) Complete genome sequence of *Leuconostoc kimchii* strain C2, isolated from kimchi. J Bacteriol 193:5548

Lee JH, Bae J-W, Chun J (2012a) Draft genome sequence of *Weissella koreensis* KCTC 3621T. J Bacteriol 194:5711–5712

Lee SH, Park MS, Jung JY, Jeon CO (2012b) *Leuconostoc miyukkimchii* sp. nov., isolated from brown algae (Undaria pinnatifida) kimchi. Int J Syst Evol Microbiol 62:1098–1103

Lefeber T, Janssens M, Moens F, Gobert W, De Vuyst L (2011) Interesting starter culture strains for controlled cocoa bean fermentation revealed by simulated cocoa pulp fermentations of cocoa-specific lactic acid bacteria. Appl Environ Microbiol 77:6694–6698

Leisner JJ, Pot B, Christensen H, Rusul G, Olsen JE, Wee BW, Muhamad K, Ghazali HM (1999) Identification of lactic acid bacteria from Chili Bo, a Malaysian food ingredient. Appl Environ Microbiol 65:599–605

Leisner JJ, Vancanneyt M, van der Meulen R, Lefebvre K, Engelbeen K, Hoste B, Laursen BG, Bay L, Rusul G, de Vuyst L, Swings J (2005) *Leuconostoc durionis* sp. nov., a heterofermenter with no detectable gas production from glucose. Int J Syst Evol Microbiol 55:1267–1270

Levata-Jovanovic M, Sandine WE (1997) A method to use *Leuconostoc mesenteroides* ssp. cremoris 91404 to improve milk fermentations. J Dairy Sci 80:11–18

Lin CW, Chen HL, Liu JR (1999) Identification and characterisation of lactic acid bacteria and yeasts isolated from kefir grains in Taiwan. Aust J Dairy Technol 54:14–18

Liu SQ (2002) A review: malolactic fermentation in wine – beyond deacidification. J Appl Microbiol 92:589–601

Liu JY, Li AH, Ji C, Yang WM (2009) First description of a novel *Weissella* species as an opportunistic pathogen for rainbow trout *Oncorhynchus mykiss* (Walbaum) in China. Vet Microbiol 136:314–320

Lönner C, Prove-Akesson K (1989) Effects of lactic acid bacteria on the properties of sour dough bread. Food Microbiol 6:19–35

Lucas PM, Claisse O, Lonvaud-Funel A (2008) High frequency of histamine-producing bacteria in the enological environment and instability of the histidine decarboxylase production phenotype. Appl Environ Microbiol 74:811–817

Lucena BT, dos Santos BM, Moreira JL, Moreira AP, Nunes AC, Azevedo V, Miyoshi A, Thompson FL, de Morais MA Jr (2010) Diversity of lactic acid bacteria of the bioethanol process. BMC Microbiol 23:298

Magnusson J, Jonsson H, Schnürer J, Roos S (2002) *Weissella soli* sp. nov., a lactic acid bacterium isolated from soil. Int J Syst Evol Microbiol 52:831–834

Maina NH, Tenkanen M, Maaheimo H, Juvonen R, Virkki L (2008) NMR spectroscopic analysis of exopolysaccharides produced by *Leuconostoc citreum* and *Weissella confusa*. Carbohydr Res 343:1446–1455

Makarova K, Slesarev A, Wolf Y, Sorokin A, Mirkin B, Koonin E, Pavlov A, Pavlova N, Karamychev V, Polouchine N, Shakhova V, Grigoriev I, Lou Y, Rohksar D, Lucas S, Huang K, Goodstein DM, Hawkins T, Plengvidhya V, Welker D, Hughes J, Goh Y, Benson A, Baldwin K, Lee JH, Díaz-Muñiz I, Dosti B, Smeianov V, Wechter W, Barabote R, Lorca G, Altermann E, Barrangou R, Ganesan B, Xie Y, Rawsthorne H, Tamir D, Parker C, Breidt F, Broadbent J, Hutkins R, O'Sullivan D, Steele J, Unlu G, Saier M, Klaenhammer T, Richardson P, Kozyavkin S, Weimer B, Mills D (2006) Comparative genomics of the lactic acid bacteria. Proc Natl Acad Sci U S A 103:15611–15616

Mäki M (2004) Lactic acid bacteria in vegetable fermentations. In: Salminen S, von Wright A, Ouwehand A (eds) Lactic acid bacteria. Microbiological and functional aspects, 3rd edn. Marcel Dekker, New York/Basel, pp 419–430

Marcobal A, Sela DA, Wolf YI, Makarova KS, Mills DA (2008) Role of hypermutability in the evolution of the genus *Oenococcus*. J Bacteriol 190:564–570

Marshall VM, Cole WM (1985) Methods for making kefir and fermented milks based on kefir. J Dairy Res 52:451–456

Martinez-Murcia AJ, Collins MD (1990) A phylogenetic analysis of the genus *Leuconostoc* based on reverse transcriptase sequencing of 16S rRNA. FEMS Microbiol Lett 70:73–84

Martinez-Murcia AJ, Harland NM, Collins MD (1993) Phylogenetic analysis of some leuconostocs and related organisms as determined from large-subunit rRNA gene sequences: assessment of congruence of small- and large-subunit rRNA derived trees. J Appl Bacteriol 74:532–541

Marty-Teysset C, Posthuma C, Lolkema JS, Schmitt P, Divies C, Konings WN (1996) Proton motive force generation by citrolactic fermentation in Leuconostoc mesenteroides. J Bacteriol 178:2178–2185

Menendez S, Godínez R, Centeno JA, Rodríguez-Otero JL (2001) Microbiological, chemical and biochemical characteristics of "Tetilla" raw cows-milk cheese. Food Microbiol 18:151–158

Mesas JM, Rodríguez MC, Alegre MT (2011) Characterization of lactic acid bacteria from musts and wines of three consecutive vintages of Ribeira Sacra. Lett Appl Microbiol 52:258–268

Meslier V, Loux V, Renault P (2012) Genome sequence of *Leuconostoc pseudomesenteroides* strain 4882, Isolated from a dairy starter culture. J Bacteriol 194:6637

Minervini F, Lattanzi A, De Angelis M, Di Cagno R, Gobbetti M (2012) Influence of artisan bakery- or laboratory-propagated sourdoughs on the diversity of lactic acid bacterium and yeast microbiotas. Appl Environ Microbiol 78:5328–5340

Monchois V, Willemot RM, Monsan P (1999) Glucansucrases: mechanism of action and structure-function relationships. FEMS Microbiol Rev 23:131–151

Morales F, Morales JI, Hernández CH, Hernández-Sánchez H (2011) Isolation and partial characterization of halotolerant lactic acid bacteria from two Mexican cheeses. Appl Biochem Biotechnol 164:889–905

Moreno-Arribas MV, Polo MC, Jorganes F, Muñoz R (2003) Screening of biogenic amine production by lactic acid bacteria isolated from grape must and wine. Int J Food Microbiol 84:117–123

Morse R, Collins MD, O'Hanlon K, Wallbanks S, Richardson PT (1996) Analysis of the beta' subunit of DNA-dependent RNA polymerase does not support the hypothesis inferred from 16S rRNA analysis that *Oenococcus oeni* (formerly *Leuconostoc oenos*) is a tachytelic (fast-evolving) bacterium. Int J Syst Bacteriol 46:1004–1009

Müller G (1996) Kaffee, Kakao, Tee, Vanile, Tabak. In: Müller G, Holzapfel WH, Weber H (eds) Mikrobiologie der Lebensmittel: Lebensmittel pflanzlicher Herkunft. Behr's Verlag, Hamburg, pp 431–450

Mundt JO (1967) Spherical lactic acid-producing bacteria of southern-grown raw and processed vegetables. Appl Environ Microbiol 15:1303–1308

Nam S-H, Choi S-H, Kang A, Kim D-W, Kim D-S, Kim RN, Kim A, Park H-S (2010a) Genome sequence of *Leuconostoc fallax* KCTC 3537. J Bacteriol 193:588–589

Nam S-H, Choi S-H, Kang A, Kim D-W, Kim RN, Kim A, Park H-S (2010b) Genome sequence of *Leuconostoc argentinum* KCTC 3773. J Bacteriol 192:6490–6491

Nam S-H, Kim A, Choi S-H, Kang A, Kim D-W, Kim RN, Kim D-S, Park H-S (2011) Genome sequence of *Leuconostoc carnosum* KCTC 3525. J Bacteriol 193:6100–6101

Nedovic VA, Durieuxb A, Van Nedervelde L, Rosseels P, Vandegans J, Plaisant A, Simon J (2000) Continuous cider fermentation with co-immobilized yeast and *Leuconostoc oenos* cells. Enzyme Microb Technol 26:834–839

Nielsen J, Prahl C, Lonvaud-Funel A (1996) Malolactic fermentation in wine by direct inoculation with freeze-dried *Leuconostoc oenos* cultures. Am J Enol Vitic 47:42–48

Nielsen DS, Teniola OD, Ban-Koffi L, Owusu M, Andersson TS, Holzapfel WH (2007) The microbiology of Ghanaian cocoa fermentations analysed using culture-dependent and culture-independent methods. Int J Food Microbiol 114:168–186

Nieto-Arribas P, Seseña S, Poveda JM, Palop L, Cabezas L (2010) Genotypic and technological characterization of Leuconostoc isolates to be used as adjunct starters in Manchego cheese manufacture. Food Microbiol 27:85–93

Niven CF Jr, Evans JB (1957) *Lactobacillus viridescens* nov. spec., a heterofermentative species that produces a green discoloration of cured meat pigments. J Bacteriol 73:758–759

Niven CF Jr, Buettner LG, Evans JB (1954) Thermal tolerance studies on the heterofermentative lactobacilli that cause greening of cured meat products. Appl Microbiol 2:26–29

Oh H-M, Cho Y-J, Kim BK, Roe J-H, Kang S-O, Nahm BH, Jeong G, Han H-U, Chun J (2010) Complete genome sequence analysis of *Leuconostoc kimchii* IMSNU 11154. J Bacteriol 192:3844–3845

Okafor N (1977) Microorganisms associated with cassava fermentation for gari production. J Appl Bacteriol 42:279–284

Okafor N, Ejiofor MAN (1985) The linamarase of *Leuconostoc mesenteroides*, production, isolation and some properties. J Sci Food Agric 36:669–678

Olano A, Chua J, Schroeder S, Minari A, La Salvia M, Hall G (2001) *Weissella confusa* (basonym: *Lactobacillus confusus*) bacteremia: a case report. J Clin Microbiol 39:1604–1607

Orberg PK, Sandine WE (1984) Common occurrence of plasmid DNA and vancomycin resistance in *Leuconostoc* spp. Appl Environ Microbiol 48:1129–1133

Ostovar K, Keeney PG (1973) Isolation and characterization of microorganisms involved in the fermentation of Trinidad's cacao beans. J Food Sci 38:611–617

Ouoba LII, Kando C, Parkouda C, Sawadogo-Lingani H, Diawara B, Sutherland JP (2012) The microbiology of Bandji, palm wine of *Borassus akeassii* from Burkina Faso: identification and genotypic diversity of yeasts, lactic acid and acetic acid bacteria. J Appl Microbiol 113(6):1428–1441

Padonou SW, Nielsen DS, Hounhouigan JD, Thorsen L, Nago MC, Jakobsen M (2009) The microbiota of Lafun, an African traditional cassava food product. Int J Food Microbiol 133:22–30

Padonou SW, Schillinger U, Nielsen DS, Franz CMAP, Hansen M, Hounhouigan JD, Nago MC, Jakobsen M (2010) *Weissella beninensis* sp. nov., a motile lactic acid bacterium from submerged cassava fermentations, and emended description of the genus *Weissella*. Int J Syst Evol Microbiol 60:2193–2198

Papalexandratou Z, Falony G, Romanens E, Jimenez JC, Amores F, Daniel HM, De Vuyst L (2011a) Species diversity, community dynamics, and metabolite kinetics of the microbiota associated with traditional ecuadorian spontaneous cocoa bean fermentations. Appl Environ Microbiol 77:7698–7714

Papalexandratou Z, Vrancken G, De Bruyne K, Vandamme P, De Vuyst L (2011b) Spontaneous organic cocoa bean box fermentations in Brazil are characterized by a restricted species diversity of lactic acid bacteria and acetic acid bacteria. Food Microbiol 28:1326–1338

Papamanoli E, Tzanetakis N, Litopoulou-Tzanetaki E, Kotzekidou P (2003) Characterization of lactic acid bacteria isolated from a Greek dry-fermented sausage in respect of their technological and probiotic properties. Meat Sci 65:859–867

Parente E, Grieco S, Crudele MA (2001) Phenotypic diversity of lactic acid bacteria isolated from fermented sausages produced in Basilicata (Southern Italy). J Appl Microbiol 90:943–952

Passos FML, Silva DO, Lopez A, Ferreira CLLF, Guimaraes WV (1984) Characterization and distribution of lactic-acid bacteria from traditional cocoa bean fermentations in Bahia, Brazil. J Food Sci 49:205–208

Pederson CS (1930) Floral changes in the fermentation of sauerkraut. N Y Agric Exp Sta Techn Bull 168:137

Pederson CS, Albury MN (1955) Variation among the heterofermentative lactic acid bacteria. J Bacteriol 70:702–708

Pereira CI, Romão MVS, Lolkema JS, Crespo MTB (2009) Weissella halotolerans W22 combines arginine deiminase and ornithine decarboxylation pathways and converts arginine to putrescine. J Appl Microbiol 107:1894–1902

Ramos A, Santos H (1996) Citrate and sugar cofermentation in *Leuconostoc oenos*, a 13^C nuclear magnetic resonance study. Appl Environ Microbiol 62:2577–2585

Reguant C, Bordons A (2003) Typification of *Oenococcus oeni* strains by multiplex RAPD-PCR and study of population dynamics during malolactic fermentation. J Appl Microbiol 95:344–353

Robert H, Gabriel V, Fontagné-Faucher C (2009) Biodiversity of lactic acid bacteria in French wheat sourdough as determined by molecular characterization using species-specific PCR. Int J Food Microbiol 135:53–59

Rodas AM, Ferrer S, Pardo I (2003) 16S-ARDRA, a tool for identification of lactic acid bacteria isolated from grape must and wine. Syst Appl Microbiol 26:412–422

Rodríguez-Nogales JM, Vila-Crespo J, Fernández-Fernández E (2012) Immobilization of *Oenococcus oeni* in Lentikats® to develop malolactic fermentation in wines. Biotechnol Prog 29(1):60–65

Rogosa M, Mitchell JA, Wiseman RF (1951) A selective medium for the isolation and enumeration of oral and faecal lactobacilli. J Bacteriol 62:132–133

Salimnia H, Alangaden GJ, Bharadwaj R, Painter TM, Chandrasekar PH, Fairfax MR (2011) *Weissella confusa*: an unexpected cause of vancomycin-resistant Gram-positive bacteremia in immunocompromised hosts. Transpl Infect Dis 13:94–98

Samelis J, Maurogenakis F, Metaxopoulos J (1994) Characterisation of lactic acid bacteria isolated from naturally fermented Greek dry salami. Int J Food Microbiol 23:179–196

Samelis J, Rementzis J, Tsakalidou E, Metaxopoulos J (1998) Usefulness of rapid GC analysis of cellular fatty acids for distinguishing *Weissella viridescens*, *Weissella paramesenteroides*, *Weissella hellenica* and some nonidentifiable, arginine negative *Weissella* strains of meat origin. Syst Appl Microbiol 21:260–265

Samelis J, Kakouri A, Pappa EC, Matijasic BB, Georgalaki MD, Tsakalidou E, Rogelj A (2010) Microbial stability and safety of traditional Greek Graviera cheese: characterization of the lactic acid bacterial flora and culture-independent detection of bacteriocin genes in the ripened cheeses and their microbial consortia. J Food Prot 73:1294–1303

Sánchez A, Coton M, Coton E, Herrero M, García LA, Díaz M (2012) Prevalent lactic acid bacteria in cider cellars and efficiency of *Oenococcus oeni* strains. Food Microbiol 32:32–37

Santos EM, Diez AM, González-Fernández C, Jaime I, Rovira J (2005) Microbiological and sensory changes in "Morcilla de Burgos" preserved in air, vacuum and modified atmosphere packaging. Meat Sci 71:249–255

São-José C, Santos S, Nascimento J, Brito-Madurro AG, Parreira R, Santos MA (2004) Diversity in the lysis-integration region of oenophage genomes and evidence for multiple tRNA loci, as targets for prophage integration in *Oenococcus oeni*. Virology 325:82–95

Sato H, Yanagida F, Shinohara T, Suzuki M, Suzuki K, Yokotsuka K (2001) Intraspecific diversity of *Oenococcus oeni* isolated during red wine-making in Japan. FEMS Microbiol Lett 202:109–114

Scheirlinck I, Van der Meulen R, Van Schoor A, Vancanneyt M, De Vuyst L, Vandamme P, Huys G (2007) Influence of geographical origin and flour type on diversity of lactic acid bacteria in traditional Belgian sourdoughs. Appl Environ Microbiol 73:6262–6269

Schillinger U, Holzapfel WH (2011) Culture media for lactic acid bacteria. In: Corry J, Curtis G, Baird R (eds) Handbook of culture media for food and water microbiology. Royal Society of Chemistry, Cambridge, UK, pp 174–192

Schillinger U, Björkroth KJ, Holzapfel WH (2006) Lactic acid bacteria. In: de Blackburn CW (ed) Food spoilage microorganisms. Woodhead, Cambridge, UK, pp 541–578 (Chap 20)

Schleifer KH (2009) Family V. *Leuconostocaceae* fam. nov. In: De Vos P, Garrity GM, Jones D, Krieg NR, Ludwig W, Rainey FA, Schleifer KH, Whitman WB (eds) Bergey's manual of systematic bacteriology (The Firmicutes), vol 3, 2nd edn. Springer, Dordrecht/Heidelberg/London/New York, p 624

Schmitt P, Mathot AG, Divies C (1989) Fatty acid composition of the genus *Leuconostoc*. Milchwissenschaft-Milk Sci Int 44:556–559

Schmitt P, Vasseur C, Phalip V, Huang DQ, Diviés C, Prevost H (1997) Diacetyl and acetoin production from the co-metabolism of citrate and xylose by *Leuconostoc mesenteroides* subsp. *mesenteroides*. Appl Microbiol Biotechnol 47:715–718

Shaw BG, Harding CD (1989) *Leuconostoc gelidum* sp. nov. and *Leuconostoc carnosum* sp. nov. from chill-stored meats. Int J Syst Bacteriol 39:217–223

Sijpesteijn AK (1970) Induction of cytochrome formation and stimulation of oxidative dissimilation by hemin in *Streptococcus lactis* and *Leuconostoc mesenteroides*. Antonie Van Leeuwenhoek 36:335–348

Snauwaert I, Papalexandratou Z, De Vuyst L, Vandamme P (2013) Characterization of *Weissella fabalis* sp. nov. and *Fructobacillus tropaeoli* from spontaneous cocoa bean fermentations. Int J Syst Evol Microbiol 63(Pt 5):1709–1716. doi:10.1099/ijs.0.040311-0

Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22:2688–2690

Stamer JR (1975) Recent developments in the fermentation of sauerkraut. In: Carr JG, Cutting CV, Whiting GC (eds) Lactic acid bacteria in beverages and food. Academic, London, pp 267–280

Stamer JR (1988) Lactic acid bacteria in fermented vegetables. In: Robinson RK (ed) Developments in food microbiology, vol 3. Elsevier, London, pp 67–85

Steinkraus KH (1983) Lactic acid fermentation in the production of foods from vegetables, cereals and legumes. Antonie Van Leeuwenhoek 49:337–348

Stiles ME, Holzapfel WH (1997) Lactic acid bacteria of foods and their current taxonomy. Int J Food Microbiol 36:1–29

Tanasupawat S, Shida O, Okada S, Komagata K (2000) *Lactobacillus acidipiscis* sp. nov. and *Weissella thailandensis* sp. nov., isolated from fermented fish in Thailand. Int J Syst Evol Microbiol 50(Pt 4):1479–1485

Tannock GW, Tilsala-Timisjarvi A, Rodtong S, Ng J, Munro K, Alatossava T (1999) Identification of Lactobacillus isolates from the gastrointestinal tract, silage, and yoghurt by 16S-23S rRNA gene intergenic spacer region sequence comparisons. Appl Environ Microbiol 65:4264–4267

Thaochan N, Drew RA, Hughes JM, Vijaysegaran S, Chinajariyawong A (2010) Alimentary tract bacteria isolated and identified with API-20E and molecular cloning techniques from Australian tropical fruit flies *Bactrocera cacuminata* and *B. tryoni*. J Insect Sci 10:1–16

Tohno M, Kitahara M, Inoue H, Uegaki R, Irisawa T, Ohkuma M, Tajima K (2012) *Weissella oryzae* sp. nov., isolated from fermented rice grain (*Oryza sativa* L. subsp. *japonica*). Int J Syst Evol Microbiol 63(Pt 4):1417–1420

Tracey RP, Britz TJ (1987) A numerical taxonomic study of *Leuconostoc oenos* strains from wine. J Appl Bacteriol 63:523–532

Tracey RP, Britz TJ (1989) Cellular fatty acid composition of *Leuconostoc oenos*. J Appl Bacteriol 66:445–456

Tu R-J, Wu H-Y, Lock Y-S, Chen M-J (2010) Evaluation of microbial dynamics during the ripening of a traditional Taiwanese naturally fermented ham. Food Microbiol 27:460–467

Van Tieghem PH (1878) Sur La Gomme De Sucrerie (*Leuconostoc mesenteroides*). Annal de Sci Nat Bot Ser 7:180–203

Vancanneyt M, Zamfir M, De Wachter M, Cleenwerck I, Hoste B, Rossi F, Dellaglio F, De Vuyst L, Swings J (2006) Reclassification of *Leuconostoc argentinum* as a later synonym of *Leuconostoc lactis*. Int J Syst Evol Microbiol 56:213–216

Vaughn RH (1985) The microbiology of vegetable fermentations. In: Wood BJB (ed) Microbiology of fermented foods, 2nd edn. Elsevier, New York, pp 49–109

Vedamuthu ER (1994) The dairy *Leuconostoc*: use in dairy products. J Dairy Sci Am Dairy Sci Assoc 77(9):2725–2737

Vela AI, Porrero C, Goyache J, Nieto A, Sanchez B, Briones V, Moreno MA, Dominguez L, Fernandez-Garayzabal JF (2003) *Weissella confusa* infection in primate (*Cercopithecus mona*). Emerg Infect Dis 9:1307–1309

Vela AI, Fernández A, de Quirós YB, Herráez P, Domínguez L, Fernández-Garayzábal JF (2011) *Weissella ceti* sp. nov., isolated from beaked whales (*Mesoplodon bidens*). Int J Syst Evol Microbiol 61:2758–2762

Vigentini I, Picozzi C, Tirelli A, Giugni A, Foschino R (2009) Survey on indigenous *Oenococcus oeni* strains isolated from red wines of Valtellina, a cold climate wine-growing Italian area. Int J Food Microbiol 136(1):123–128

Vihavainen EJ, Johanna Björkroth K (2009) Diversity of *Leuconostoc gasicomitatum* associated with meat spoilage. Int J Food Microbiol 136(1):32–36

von Weymarn FNW, Kiviharju KJ, Jääskeläinen ST, Leisola MSA (2003) Scale-up of a new bacterial mannitol production process. Biotechnol Prog 19:815–821

Walker DK, Gilliland SE (1987) Buttermilk manufacture using a combination of direct acidification and citrate fermentation by *Leuconostoc cremoris*. J Dairy Sci 70:2055–2062

Walter J, Hertel C, Tannock GW, Lis CM, Munro K, Hammes WP (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

Wibowo D, Eschenbruch R, Davis CR, Fleet GH, Lee TH (1985) Occurrence and growth of lactic-acid bacteria in wine: a review. Am J Enol Viticult 36:302–313

Williams AM, Collins MD (1990) Molecular taxonomic studies on *Streptococcus uberis* types I and II. Description of *Streptococcus parauberis* sp. nov. J Appl Bacteriol 68:485–490

Yanagida F, Yi-Sheng C, Masatoshi Y (2007) Isolation and characterization of lactic acid bacteria from lakes. J Basic Microbiol 47:184–190

Yang D, Woese CR (1989) Phylogenetic structure of the "Leuconostocs": an interesting case of a rapidly evolving organism. Syst Appl Microbiol 12(2):145–149

Yarza P, Ludwig W, Euzéby J, Schleifer K-H, Amann R, Amann R, Glöckner FO, osselló-Móra R (2010) Update of the all-species living tree project based on 16S and 23S rRNA sequence analyses. Syst Appl Microbiol 33:291–299

Yu J, Wang WH, Menghe BLG, Jiri MT, Wang HM, Liu WJ, Bao QH, Lu Q, Zhang JC, Wang F, Xu HY, Sun TS, Zhang HP (2011) Diversity of lactic acid bacteria associated with traditional fermented dairy products in Mongolia. J Dairy Sci 94:3229–3241

Zakaria Y, Ariga H, Urashima T, Toba T (1998) Microbiological and rheological properties of the Indonesian traditional fermented milk Dadih. Milchwissenschaft 53:30–33

Zamudio-Maya M, Narváez-Zapata J, 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

Zapparoli G, Reguant C, Bordons A, Torriani S, Dellaglio F (2000) Genomic DNA fingerprinting of *Oenococcus oeni* strains by pulsed-field gel electrophoresis and randomly amplified polymorphic DNA-PCR. Curr Microbiol 40:351–355

Zapparoli G, Fracchetti F, Stefanelli E, Torriani S (2012) Genetic and phenotypic strain heterogeneity within a natural population of *Oenococcus oeni* from Amarone wine. J Appl Microbiol 113:1365–2672

Zaunmüller T, Eichert M, Richter H, Unden G (2006) Variations in the energy metabolism of biotechnologically relevant heterofermentative lactic acid bacteria during growth on sugars and organic acids. Appl Microbiol Biotechnol 72:421–429

Zavaleta AI, Martinez-Murcia AJ, Rodriguez-Valera F (1996) 16S–23S rDNA intergenic sequences indicate that *Leuconostoc oenos* is phylogenetically homogeneous. Microbiology 142:2105–2114

Zickrick K (1996) Mikrobiologie der Käse. In: Weber H (ed) Mikrobiologie der Lebensmittel: Milch und Milchprodukte. Behr's Verlag, Hamburg, pp 255–351