Chapter 1
Lactic Acid Bacteria

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1.1 Introduction

In 1873, ten years after L. Pasteur studied lactic acid fermentation (between 1857 and 1863), the first pure culture of a lactic acid bacterium (LAB) ("*Bacterium lactis*") was obtained by J. Lister. Starter cultures for cheese and sour milk production were introduced in 1890, while fermented food has been used by man for more than 5,000 years (Schlegel 1999; Stiles and Holzapfel 1997). The first monograph by S. Orla-Jensen appeared in 1919. A typical lactic acid bacterium grown under standard conditions (nonlimiting glucose concentration, growth factors and oxygen limitation) is gram-positive, nonsporing, catalase negative in the absence of porphorinoids, aerotolerant, acid tolerant, organotrophic, and a strictly fermentative rod or coccus, producing lactic acid as a major end product. It lacks cytochromes and is unable to synthesize porphyrins. Its features can vary under certain conditions. Catalase and cytochromes may be formed in the presence of hemes and lactic acid can be further metabolized, resulting in lower lactic acid concentrations. Cell division occurs in one plane, except pediococci. The cells are usually nonmotile. They have a requirement for complex growth factors such as vitamins and amino acids. An unequivocal definition of LAB is not possible (Axelsson 2004).

Lactic acid bacteria are characterized by the production of lactic acid as a major catabolic end product from glucose. Some bacilli, such as *Actinomyces israeli* and bifidobacteria, can form lactic acid as a major end product, but these bacteria have rarely or never been isolated from must and wine. The DNA of LAB has a G + C content below 55 mol%. LAB are grouped into the *Clostridium* branch of gram-positive bacteria possessing a relationship to the bacilli, while *Bifidobacterium* belongs to the Actinomycetes. They are grouped in one order and six families. From the 32 described genera, only 22 species belonging to five genera have been isolated from must and wine (Table 1.1).

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The homofermentative species produce lactic acid (<85%) as the sole end product, while the heterofermentative species produce lactic acid, CO_2 and ethanol/acetate. At least half of the end product carbon is lactate. Heterofermentative LAB utilizes the pentose phosphate pathway, alternatively referred to as the phosphoketolase or phosphogluconate pathway. Homofermentative wine-related LAB include pediococci and group I lactobacilli. Obligate heterofermentative wine-related LAB include *Leuconostoc*, *Oenococcus*, *Weissella* and group III lactobacilli (Tables 1.2–1.5).

Table 1.1 Current taxonomic outline of lactic acid bacteria[a] of the *Clostridium* branch

Phylum Class Order	Family	Genus	Species from Must and Wine
"Firmicutes" "Bacilli" "Lactobacillales"	I. Lactobacillaceae	I. *Lactobacillus*	*Lb. brevis*, *Lb. buchneri*, *Lb. casei*, *Lb. curvatus*, *Lb. delbrueckii*, *Lb. diolivorans*, *Lb. fermentum*, *Lb. fructivorans*, *Lb. hilgardii*, *Lb. jensenii*, *Lb. kunkeei*, *Lb. mali*, *Lb. nagelii*, *Lb. paracasei*, *Lb. plantarum*, *Lb. vini*
		II. *Paralactobacillus*	
		III. *Pediococcus*	*P. pentosaceus*, *P. parvulus*, *P. damnosus*
	II. "Aerococcaceae"	I. *Aerococcus*	
		II. *Abiotrophia*	
		III. *Dolosicoccus*	
		IV. *Eremococcus*	
		V. *Facklamia*	
		VI. *Globicatella*	
		VII. *Ignavigranum*	
	III. "Carnobacteriaceae"	I. *Carnobacterium*	
		II. *Agitococcus*	
		III. *Alkalibacterium*	
		IV. *Allofustis*	
		V. *Alloiococcus*	
		VI. *Desemzia*	
		VII. *Dolosigranulum*	
		VIII. *Granulicatella*	
		IX. *Isobaculum*	
		X. *Lactosphaera*	
		XI. *Marinilactibacillus*	
		XII. *Trichococcus*	

(continued)

Table 1.1 (continued)

Phylum Class Order	Family	Genus	Species from Must and Wine
	IV. "Enterococcaceae"	I. *Enterococcus*	
		II. *Atopobacter*	
		III. *Melissococcus*	
		IV. *Tetragenococcus*	
		V. *Vagococcus*	
	V. "Leuconostocaceae"	I. *Leuconostoc*	*Lc. mesenteroides*
		II. *Oenococcus*	*O. oeni*
		III. *Weissella*	*W. paramesenteroides*
	VI. Streptococcaceae	I. *Streptococcus*	
		II. *Lactococcus*	

[a]Garrity GM (2005). Principal genera of LAB are underlined (Axelsson 2004)

Table 1.2 Differential characteristics of the wine-related lactic acid genera

Genus	Morphology from Glc	Carbohydrate fermentation[a]	Lactic acid isomer
Lactobacillus	Rods, coccobacilli cells single or in chains	homo- or heterofermentative facultatively heterofermentative	D, L, DL
Leuconostoc[b]	Spherical or lenticular cells in pairs or chains	heterofermentative	D
Oenococcus[b]	Spherical or lenticular cells in pairs or chains	heterofermentative	D
Pediococcus	Spherical cells, pairs or tetrads	homofermentative or facultatively heterofermentative[c]	DL, L
Weissella	Spherical, lenticular, irregular cells	heterofermentative	D, DL

[a]nonlimiting concentration of glucose and growth factors, but oxygen limitation.
[b]Differentiation of wine-related species of *Leuconostoc* and *Oenococcus* cf. Table 1.4.
[c]Facultatively heterofermentative species: *P. pentosaceus, P. acidilactici, P. claussenii.*

Our present knowledge about LAB in general (Carr et al. 1975; Wood and Holzapfel 1995; Holzapfel and Wood 1998; Wood 1999; Wood and Warner 2003; Salminen et al. 2004) and their activities on grape or in must and wine (Fleet 1993; Dittrich and Großmann 2005; Ribéreau-Gayon et al. 2006a, b; Fugelsang and Edwards 2007) has been compiled in several books.

1.2 Ecology

In general, LAB occur in habitats with a rich nutrition supply. They occur on decomposing plant material and fruits, in dairy products, fermented meat and fish, beets, potatoes, mash, sauerkraut, sourdough, pickled vegetables, silage, beverages, plants, water, juices, sewage and in cavities (mouth, genital, intestinal and respiratory tract) of human and animals. They are part of the healthy microbiota of the

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