



## Review

# From field to fermentation: The origins of *Lactococcus lactis* and its domestication to the dairy environment



Daniel Cavanagh<sup>a, b, \*</sup>, Gerald F. Fitzgerald<sup>b</sup>, Olivia McAuliffe<sup>a</sup>

<sup>a</sup> Teagasc Food Research Centre, Moorepark, Fermoy, Co. Cork, Ireland

<sup>b</sup> Department of Microbiology, University College Cork, Co. Cork, Ireland

## ARTICLE INFO

## Article history:

Received 28 July 2014

Received in revised form

22 October 2014

Accepted 1 November 2014

Available online 11 November 2014

## Keywords:

*Lactococcus*

Amino acid auxotrophy

Comparative genomics

Sugar metabolism

Environments

## ABSTRACT

*Lactococcus lactis* is an organism of substantial economic importance, used extensively in the production of fermented foods and widely held to have evolved from plant strains. The domestication of this organism to the milk environment is associated with genome reduction and gene decay, and the acquisition of specific genes involved in protein and lactose utilisation by horizontal gene transfer. In recent years, numerous studies have focused on uncovering the physiology and molecular biology of lactococcal strains from the wider environment for exploitation in the dairy industry. This in turn has facilitated comparative genome analysis of lactococci from different environments and provided insight into the natural phenotypic and genetic diversity of *L. lactis*. This diversity may be exploited in dairy fermentations to develop products with improved quality and sensory attributes. In this review, we discuss the classification of *L. lactis* and the problems that arise with phenotype/genotype designation. We also discuss the adaptation of non-dairy lactococci to milk, the traits associated with this adaptation and the potential application of non-dairy lactococci to dairy fermentations.

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## 1. Introduction

The lactic acid bacteria (LAB) comprise a group of Gram-positive organisms which are primarily anaerobic, non-sporulating bacteria which produce lactic acid as the principal end product of sugar fermentation (Kandler and Weiss, 1986). Numerous species of bacteria are capable of producing lactic acid but the term LAB is restricted to specific genera including *Lactococcus* amongst others (Stiles and Holzapfel, 1997). LAB have been exploited for thousands of years in the production of fermented foods whereby they contribute to flavour, quality, texture and safety of the products (Settanni and Corsetti, 2008). While these organisms produce mainly lactic acid as a by-product of sugar fermentation (homo-fermentation), there are many examples of heterofermenting LAB, producing an array of different fermentation products including ethanol, carbon dioxide, acetic acid and formic acid (Kleerebezem and Hugenholtz, 2003). Among the most widely selected genera for industrial application are *Oenococcus* (wine), *Lactobacillus*

(meat, vegetables, dairy, cereals) and *Lactococcus* (dairy) (Bourdichon et al., 2012). Two species of *Lactococcus* are listed in the 'Inventory of Microbial Food Cultures' with documented use in food fermentations, *Lactococcus raffinolactis* and *Lactococcus lactis* (Bourdichon et al., 2012).

*L. lactis* is the main constituent of dairy starter culture systems used worldwide for the production of numerous fermented dairy products including cheese of both artisanal and commercial origin, and fermented milks such as buttermilk and sour cream. Indeed, through the consumption of fermented dairy products, it is estimated that humans ingest up to  $10^{18}$  lactococcal cells per annum (Mills et al., 2010). Based on its history of use in food fermentations, *L. lactis* has GRAS, or Generally Regarded As Safe, status (FDA, 2010). The predominant role of *L. lactis* in dairy starter cultures is to produce lactic acid at a sufficient rate and contribute to the breakdown of milk proteins during fermentation (Wouters et al., 2002), thus significantly contributing to the final product in terms of organoleptic properties and microbial quality (Ross et al., 2000). A small number of *L. lactis* strains are routinely used in fermented food production in an effort to develop more consistent products. These strains are chosen primarily for their acidification activity and resistance to bacteriophage infection (Marshall, 1991). However, consumer demands for products of more diverse flavour

\* Corresponding author. Food Biosciences Department, Teagasc Food Research Centre, Moorepark, Fermoy, Co. Cork, Ireland. Tel.: +353 25 42568.

E-mail addresses: [daniel.cavanagh@teagasc.ie](mailto:daniel.cavanagh@teagasc.ie) (D. Cavanagh), [g.fitzgerald@ucc.ie](mailto:g.fitzgerald@ucc.ie) (G.F. Fitzgerald), [olivia.mcauliffe@teagasc.ie](mailto:olivia.mcauliffe@teagasc.ie) (O. McAuliffe).

is driving manufacturers of fermented dairy products to expand their culture systems. These new cultures must be able to create desirable products in terms of flavour and texture while also enduring the environmental stresses associated with the manufacture of fermented dairy foods (Mills et al., 2010). The creation of genetically modified organisms (GMOs) has the potential to resolve this problem, but the introduction of such organisms into the food chain is met with much opposition from both governmental agencies and consumers alike (Pedersen et al., 2005). An alternative non-GM approach is through the examination of the natural biodiversity which exists in the LAB group, including *L. lactis* from outside the dairy environment. Such an approach may provide a means to identify novel starter cultures with the desired industrial traits for production in terms of flavour development and bacteriophage resistance (Ayad et al., 2000; Mills et al., 2010).

A high degree of sequence similarity exists between Streptococcaceae, yet they can be found in a broad range of different environmental niches. Members of the *Lactococcus* genus can be isolated from raw-milk, raw-milk cheeses and non-milk environments and are collectively referred to as 'wild-type'. Indeed, strains of *L. lactis* have been isolated from a range of sources including drain water and human vaginal samples (Gao et al., 2011; Kato et al., 2012). Although not a common resident of the gastro intestinal tract (GIT), *L. lactis* is capable of surviving gut passage (Kimoto et al., 1999; Meyrand et al., 2013). This in turn has opened up the potential of these strains for probiotic use, and the delivery of therapeutic drugs *in-vivo* (Steidler and Rottiers, 2006; Wells and Mercenier, 2008) and the targeted delivery of vaccines by this organism has been examined (Asensi et al., 2013). In recent years the number of sequenced lactococcal strains from different environmental niches has grown considerably (Table 1). This has shed further light on the diversity within the *L. lactis* species and identified genes present in these strains which may be harnessed to impart added value to dairy fermentations. The aim of this review is to discuss the potential origins and natural diversity of *L. lactis*, and to highlight the mechanisms by which this industrially important organism has become adapted to the dairy environment. The potential features present in strains of *L. lactis* from outside the dairy

environment which could be beneficial in dairy fermentations are also highlighted.

## 2. Diverse niches of *L. lactis*

LAB are often referred to as fastidious organisms, found in nutrient rich habitats; however, in such environments these bacteria can be exposed to extremes of pH, differing nutrient availability and challenges from other microbiota for resources (Van De Guchte et al., 2002). *L. lactis* possesses a wide ecological distribution from sourdough bread (Passerini et al., 2013a), to sugar cane plants (Serna Cock and Rodríguez De Stouvenel, 2006) to the GIT of brown trout (Pérez et al., 2011). Recently, the genome sequence of *L. lactis* ssp. *lactis* IO-1, isolated from drain water, has been elucidated which possesses the capacity to utilise xylose and generates increased levels of L-lactic acid (Kato et al., 2012). Although *L. lactis* may naturally inhabit many different environments (see Table 1 for origins of sequenced strains), it is most widely known for its association with the milk environment and in the production of dairy products. Based on multi-locus sequence typing (MLST) and the formation of clonal complexes, Passerini et al. (2010) proposed that *L. lactis* strains be classed as 'domesticated' or 'environmental' in reference to their origin. Domesticated strains are thus defined as strains used as dairy starters, in milk production and found in fermented products, while environmental strains are defined as isolates from plants, animals and raw-milk.

The consensus is that industrial dairy strains used in production today are believed to be descended from plants (Kelly et al., 2010) and have adapted over time to thrive in milk. It is plausible that this species initially colonised milk from contact with grass or other plants which would have been used as fodder or bedding for cattle. *L. lactis* is one of the first bacteria to occupy plant material, where it becomes the less dominant species as the pH of the environment lowers (Kelly et al., 1998b; Kelly and Ward, 2002). It is thought that these bacteria initially colonised seeds, prior to germination, which enables them to quickly establish themselves as the dominant microbial community (Kelly et al., 1998b). This in turn may be aided by the production of anti-microbial compounds, as numerous strains isolated from plant matter have been found to produce nisin

**Table 1**  
List of available *Lactococcus lactis* genomes. Data was collected from Genbank (<http://www.ncbi.nlm.nih.gov/genome/?term=Lactococcus+lactis>; accessed 2nd July 2014).

Strain	Year	Genotype	Origin	Size (mb)	Proteins	Plasmid	G/C content (%)	Reference
<i>L. lactis</i> IL1403	2001	<i>lactis</i>	Dairy	2.37	2.277	0	35.3	(Bolotin et al., 2001)
<i>L. lactis</i> KF147	2010	<i>lactis</i>	Mung bean sprouts	2.60	2.578	1	34.9	(Siezen et al., 2010)
<i>L. lactis</i> KF282	2010	<i>lactis</i>	Mustard and cress	–	–	–	–	(Siezen et al., 2010)
<i>L. lactis</i> CV56	2011	<i>lactis</i>	Vaginal flora	2.40	2.301	5	35.2	(Gao et al., 2011)
<i>L. lactis</i> CNCMI-1631	2011	<i>lactis</i>	Fermented milk	2.51	2.579	–	34.9	(McNulty et al., 2011)
<i>L. lactis</i> IO-1	2012	<i>lactis</i>	Drain water	2.42	2.224	–	35.1	(Kato et al., 2012)
<i>L. lactis</i> YF11	2013	<i>lactis</i>	Fermented corn	2.53	2.531	0	34.8	(Du et al., 2013)
<i>L. lactis</i> NCDO 2118	2013	<i>lactis</i>	Frozen peas	2.81	n/a	–	35.0	(unpublished)
<i>L. lactis</i> TIFN2	2013	<i>lactis</i>	Dairy-cheese	2.51	2.521	–	35.1	(Erkus et al., 2013)
<i>L. lactis</i> TIFN4	2013	<i>lactis</i>	Dairy-cheese	2.55	2.598	–	35.0	(Erkus et al., 2013)
<i>L. lactis</i> KLDS 4.0325	2013	<i>lactis</i>	Fermented horse milk	2.59	2.587	3	35.4	(Yang et al., 2013)
<i>L. lactis</i> Dephy 1	2013	<i>lactis</i>	Undefined	2.60	2.686	–	35.1	(unpublished)
<i>L. lactis</i> A12	2013	<i>lactis</i>	Sourdough bread	2.70	2.725	–	35.3	(Passerini et al., 2013a)
<i>L. lactis</i> LD61	2014	<i>lactis</i>	Dairy-cheese	2.60	2.601	6	36.4	(Falentin et al., 2014)
<i>L. lactis</i> SK11	2006	<i>cremoris</i>	Dairy-cheese	2.44	2.381	4	35.9	(Makarova et al., 2006)
<i>L. lactis</i> MG1363	2007	<i>cremoris</i>	Dairy	2.53	2.434	0	35.7	(Wegmann et al., 2007)
<i>L. lactis</i> NZ9000	2010	<i>cremoris</i>	Dairy	2.53	2.510	0	35.7	(Linares et al., 2010)
<i>L. lactis</i> A76	2012	<i>cremoris</i>	Dairy-cheese	2.45	2.643	4	35.9	(Bolotin et al., 2012)
<i>L. lactis</i> KW2	2013	<i>cremoris</i>	Fermented corn	2.43	2.268	0	35.7	(Kelly et al., 2013)
<i>L. lactis</i> TIFN1	2013	<i>cremoris</i>	Dairy-cheese	2.68	2.754	–	35.5	(Erkus et al., 2013)
<i>L. lactis</i> TIFN3	2013	<i>cremoris</i>	Dairy-cheese	2.73	2.891	–	35.5	(Erkus et al., 2013)
<i>L. lactis</i> TIFN5	2013	<i>cremoris</i>	Dairy-cheese	2.54	2.232	–	35.5	(Erkus et al., 2013)
<i>L. lactis</i> TIFN7	2013	<i>cremoris</i>	Dairy-cheese	2.63	2.505	–	35.6	(Erkus et al., 2013)
<i>L. lactis</i> UC509.9	2013	<i>cremoris</i>	Dairy	2.25	2.208	8	35.9	(Ainsworth et al., 2013)
<i>L. lactis</i> HP <sup>T</sup>	2014	<i>cremoris</i>	Dairy	2.27	2.374	7	36.7	(Lambie et al., 2014)

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