Review - Pregledni rad UDK: 579.864.1

The influence of gene transfer on the lactic acid bacteria evolution

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Received - Prispjelo: 07.04.2009.
Accepted - Prihvaćeno: 09.07.2009.

Summary

In the case of preparing various dairy products, the exploitation of lactic acid bacteria has been essential in the course of past millennia in all known nations. Numerous comparative analyses of gene and genome sequences reveal that the exchange of genetic material within and between bacterial species is far more general and frequent than has previously been thought. Consequently, the horizontal gene transfer between distant species or within the same species is an important factor in the *Lactobacillales* evolution. Knowledge about the exchange of lactobacillus genetic information through horizontal gene transfer, mobile genetic elements, and its evolution is very important due to characterizations and stability maintenance of autochthonous as well as industrial lactic acid bacteria strains in dairy products that benefit human health.

Key words: the lactic acid bacteria, horizontal gene transfer, mobile genetic elements, evolution

Introduction

The lactic acid bacteria (LAB) are probably the most numerous group of bacteria linked to humans. They include extremely beneficial nonpathogenic species that are used for industrial fermentation of dairy products, bread, meats, vegetables and cereals, as well as for preparing lots of traditional dairy products. The definition of the LAB is biological rather than taxonomical, i. e. the LAB do not comprise a monophyletic group of bacteria. Most of the LAB pertain to the order *Lactobacillales*, a group of non-sporulating Gram-positive bacteria, however a few LAB species belong to the *Actinobacteria* (Schleifer and Ludwig, 1995). The *Lactobacillales* have relatively small genomes which characterize the genome size around 2 mega bases with the number of genes in different species within the range from around 1,600 to 3,000 genes (Makarova and Koonin, 2007). This variation in the number of genes and high number of pseudogenes in the dairy LAB (O'Sullivan et al., 2009) suggests that the evolution of the LAB involved processes of gene loss or decay, duplication, and acquisition (Callanan et al., 2008; Nicolas et al., 2007). Furthermore, the mosaic structures of genetic material in bacterial genomes imply a constant flow of genetic information. Although they do not undergo sexual reproduction, bacterial cells perform processes in which genetic material from one cell or environment can be incorporated into another cell forming recombinants. This horizontal gene transfer (HGT) includes: conjugation, which requires cell to cell contact, transduction - bacteriophage - facilitated transfer of genetic information, and transformation, which is the uptake of free DNA from the environment. Usually the genes to be transferred are part of mobile genetic elements, pieces of DNA that encode proteins

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important to facilitate movement of DNA within or between genomes. In this review the role of mobile genetic elements and horizontal gene transfer in *Lactobacillales* and new aspects of adaptation and diversification based on gene acquisition will be discussed.

Genome of lactic acid bacteria

Like in other bacteria, numerous complete genome sequencing data of LAB indicate that their genomes consist of a core genome and an auxiliary genome (Rasmussen et al., 2008). The essence of a species is core genome which encodes all housekeeping genes necessary for basic cellular functions that are essential for a given species and responsible for maintaining a species identity. The diversity of a species is represented by auxiliary region that encodes functions not strictly required for growth or replication but that add competitive advantage in certain ecological niches (Ochman et al., 2000). Auxiliary genes typically encode accessory functions such as the transport and use of certain non-essential nutrients, or encode supplementary biochemical pathways, are associated with bacteriophage or other mobile elements, and certain cell-surface modifications that probably relate to phage or predator resistance, but many have no known function. Their roles are to encode novel metabolic function, antibiotic resistance, bacteriocin production, and other adaptation to an ever-changing environment (Fuhrman, 2009). These genes are transferred, yielded or lost much often than the core genes. Furthermore, there is an opinion that the average rate of evolution for auxiliary genes should be extreme, while on average, the core genes will manifest a neutral rate of evolution (Riley and Lizotte-Waniewski, 2009). The genetic maps obtained for the LAB have provided an impressive demonstration of their genome plasticity (Lerat et al., 2005; Gogarten and Townsend, 2005; Claesson et al., 2007). The genome sequence of *Lactobacillus delbrueckii* ssp. *bulgaricus* has been showing the signs of ongoing specialization, with a substantial number of pseudogenes incomplete for metabolic pathways and rapid genome evolution (van de Guchte et al., 2006.) In the LAB, the adaptive evolution occurs mostly by HGT and by intracellular activity of mobilome (Lapierre et al., 2002; Teuber et al., 2003).

Mobilome of lactic acid bacteria

Mobilome, namely mobile genetic elements are major contributing factors to the generation of genetic diversity in prokaryotic organisms. They play an essential role in the evolution of bacterial genomes (Fraser et al., 2007), and are the framework of horizontal gene transfer (Siefert, 2009.). These mobile genetic elements include bacteriophages, plasmids, integrons, genomic islands, transposons and insertion sequences (Berg and Kurland, 2002; Haig and Kazazian, 2004; Siefert, 2009). Numerous transposable elements, plasmids, and phages were found in the LAB. The functions of these LAB mobile genetic elements include metabolism of carbohydrates, amino acids and citrate, hydrolysis of proteins, production of exopolysaccharides and bacteriocins, resistance to antibiotics and heavy metals, phage resistance and DNA restriction and modification systems (Gasson and Shearman, 2003; O'Driscoll et al., 2006).

Integron is a unique type of mobilome that utilizes site-specific recombination system capable of integrating and expressing modular structure named mobile gene cassettes. These cassettes are the smallest known mobilizable elements that possess a unique integrase sequence (Labbate et al., 2009). Integrons were found in association with a variety of antibiotic resistance genes (Stokes and Hall, 1989) and can be located on other mobile genetic elements such as plasmids or transposons (Nesvera et al., 1998). Besides, group II introns are self-splicing mobile retroelements (Siefert, 2009). Belhocine et al. (2004) have shown that the Ll.LtrB group II intron, originally discovered on an *Lactococcus lactis* conjugative plasmid (pRS01) and within a chromosomally located sex factor in *Lc. lactis* 712 invaded new sites using both retrohoming and retrotransposition pathways after its transfer by conjugation.

Insertion sequences (ISs) are the simplest type of mobile genetic elements that encode transposase, protein important for the mediation of movement of IS within or between bacterial genomes, and proteins for its regulation. ISs characteristically terminate a small flanking inverted repeat sequences for the establishment of site-specific recombination at the transposition site. They are a significant source of new mutations due to their variable number and different locations in bacterial genomes (Cooper et

al., 2001; Schneider et al., 2002; de Visser et al., 2004; Schneider and Lenski, 2004). Mutations mediated by ISs can cause genomic rearrangements and/or diverse effects on gene expression (Hall, 1999; Bongers et al., 2003). Some authors have reported that IS transposition may occur at higher rates in bacteria under various stressful conditions (de Visser et al., 2004; Ohtsubo et al., 2005; Twiss et al., 2005), but also in no stressful environments (Papadopoulos et al., 1999).

They form an integral part of LAB chromosome and their extrachromosomal elements such as plasmids and bacteriophages. ISs have been shown to specifically contribute to niche adaptation by promoting a variety of genetic rearrangements (Gasson and Shearman, 2003).

Large transposable elements, DNA transposons (Tn) in addition to the gene for transposase and repeat sequences carry genes for one or more proteins imparting resistance to antibiotics. These elements can move and rearrange chromosomal DNA in the cell, either by move from cell to cell through plasmids, phages, or their derivatives called integrative conjugative elements (Frost et al., 2005). Integrative conjugative transposons bear genes allowing them to transfer themselves from one bacterium to another by excising themselves to form a covalently closed circular intermediate. In the state of intracellular transposition this circular intermediate is reintegrated in the same cell or in another cell by intercellular transposition. It is transferred by conjugation to a recipient by integration into the recipient's genome (Salyers et al., 1995). Conjugative transposons have a broad host range, and they contribute to the spread of antibiotic resistance genes. This term was first used to describe tetracicycline resistance Tn *916* from *Enterococcus faecalis*, and its transfer requires a series of genes located at the right end of the transposon (Flannagan et al., 1994). Furthermore, unrelated conjugative transposon Tn*5276* from *Lactococcus lactis* integrates into at least five chromosomal sites in *Lc. lactis* MG1614, and encodes the production of and immunity to nisin, a lanthionine-containing peptide with antimicrobial activity, and the capacity to utilize sucrose (Rauch and de Vos, 1992). Integrative conjugative transposons were first found in Gram-positive cocci but are now known to be present in a variety of Gram-positive bacteria.

Plasmids are self-replicating DNA molecules existing in cells as extrachromosomal replicons. Similarly to prokaryotic chromosomes, plasmids carry origin of replication (unique core genes), and encode at least some of the proteins involved in the plasmid replication and partitioning. Its auxial genes engage homologous or non-homologous recombination with the chromosome (Frost et al., 2005). They are found in bacteria from different environments such as soil, sea, fresh water and hot spring. The presence of plasmids in lactococci was first reported by McKay at al. (1972). Presence of plasmids is common in enterococci, lactococci, leuconostocs, pediococci and rarely in some strains of lactobacilli and bifidobacteria (Mathur and Singh, 2005). The LAB often contain different numbers (from 1 to 16) of plasmids in a single strain. Although plasmids are usually not vital elements of the cell, some carry genes that are essential for survival of the host under particular environmental conditions. For instance, plasmids in the LAB have been associated with lactose fermentation (Cords et al., 1974; Siezen et al., 2005), citrate permease activity (Kempler and McKay, 1981), proteolytic activity (Otto et al., 1982), phage resistance based on restriction/modification (Sanders and Klaenhammer, 1981) or by antisense RNA inhibition (Sturino and Klaenhammer, 2002), production of bacteriocins (Fuchs et al., 1975; Akcelik, 1999; Corr et al., 2007), and conjugative transfer (Gasson and Shearman, 2003). Nevertheless, most plasmids in the genus *Lactobacillus* and *Bifidobacterium* remain cryptic (Gasson and Shearman, 2003). In addition, Wang and Lee (1997) reported that about 38 % of *Lactobacillus* species contain plasmids of different sizes (from 1.2 to 150 kb) and variable numbers (1 or more). Furthermore, genome analysis of probiotic *Lactobacillus salivarius* subspecies *salivarius* UCC118 showed 242 kb megaplasmid, pMP118 (Claesson et al., 2006).

Conjugative plasmids have evolved optimizing regulatory system for self-transmission by a conjugative transfer apparatus (Grohmann et al., 2003). They are commonly found in starter cultures of lactococci and can be transferred to recipient strains at frequencies as high as 10^{-2} (Coakley et al., 1997). Furthermore, streptococcal conjugative plasmid pIP501 has capacity to be transmitted among numerous Gram-positive strains (Langella et al.,

1993), while the broad-host-range plasmid pAM beta 1 (encoding erythromycin resistance) can be transferred by conjugation from *Streptococcus lactis* to *Lactobacillus reuteri*, *Lactobacillus murinus* and *Lactobacillus fermentum* (Tannock, 1987).

Phages from lactococci have been extensively studied due to their importance in the dairy industry. Lactococcal phages are found in raw milk and can survive pasteurization (Sanders, 1988; Madera et al., 2004). Numerous lactococcal phages have been isolated and characterized due to their negative effects on fermentation as well as their biodiversity within this ecological niche (Stanley et al., 2003). Till today all known *Lc. lactis* phages have a double-stranded genetic (DNA) material and a no contractile tail. *Lc. lactis* phages are members of the *Caudovirales* order according to the International Committee on Taxonomy of Viruses. This bacteriophage order is extremely large, morphologically and genetically diverse group that includes over 95 % of all known viruses (Maniloff and Ackermann, 1998).

Horizontal gene transfer in lactic acid bacteria

Horizontal or lateral gene transfer is the flow of genetic information between bacterial cells and it differs from the transfer of DNA from mother to daughter cell (Madigan et al., 1997). It is an integral factor in the generation of genetic variability and genome evolution in bacteria, enabling species to quickly adapt to environmental variations (Gogarten et al., 2002.) and an active mechanisms to modulate acquisition of new DNA (Fall et al., 2007). HGT has been identified in many bacterial species, by phylogenetic or compositional method, in a variety of bacterial habitats ranging from soils to biofilms to the gastrointestinal tract (Zaneveld et al., 2008). The LAB typically obtain new DNA sequences by three methods which play a part in HGT events in bacteria, namely, transformation, transduction, and conjugation (Kurland et al., 2003; Thomas and Nielsen, 2005).

Firstly, transformation is the stable uptake, integration and expression of extracellular DNA that occurs in nature when bacterial species are in a

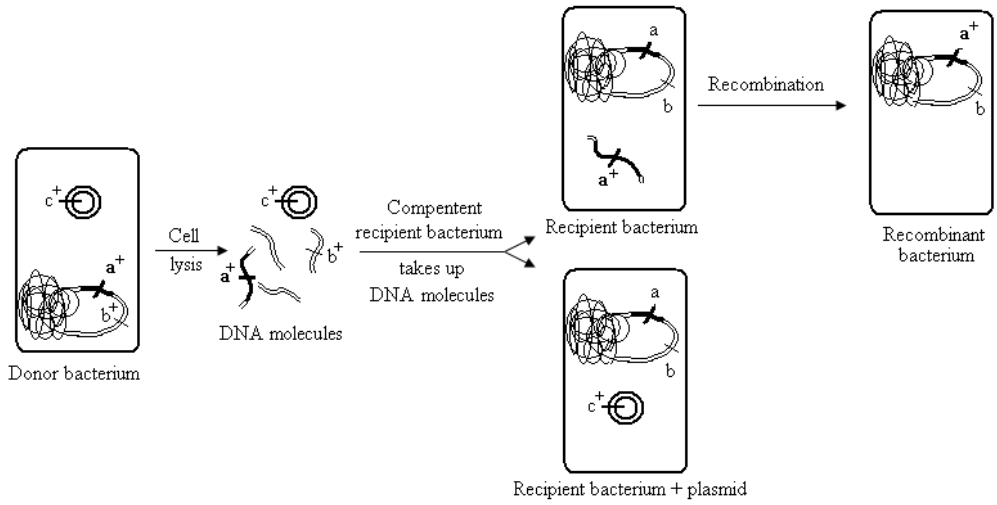

Figure 1: Schematic display of lactic acid bacteria transformation. After autolysis of a donor bacterium, naked circular or/and linear DNA molecules remain in environment. The transfer of DNA molecule to a recipient cell could result in recipient bacterium with plasmid or follow by recombination of linear DNA in the recipient chromosome. Scheme is modified from Tamarin (2002.) and Zaneveld et al. (2008)

Slika 1: Shematski prikaz transformacije u bakterija mliječne kiseline. Samorazgradnjom bakterije davatelja u okolišu ostaje nezaštićena kružna ili/i linearna molekula DNA. Prijenosom molekule DNA u stanicu primatelja može se dobiti bakterija primatelj s plazmidom ili doći do rekombinacije linearne DNA u kromosom primatelja. Prilagođeno prema Tamarin (2002.) i Zaneveld et al. (2008.)

physiological state known as competence (de la Cruz and Davies, 2000). In this process exogenous DNA which is taken up by a recipient cell and may be incorporated into the chromosome or into a plasmid by homologous or illegitimate recombination (figure 1). Transforming DNA may be a fragment of chromosomal DNA from a related strain, a plasmid, or a viral genome. Furthermore, the size of the transferred region depends on the intact DNA size during transformation. Natural transformation has been also shown in many bacteria and archaea. Trieu-Cuot et al. (1987) for the first time reported *in vitro* transfer of the plasmid pAT187 from Gram-negative *E. coli* to the Gram-positive strains: *Enteroccoccus faecalis*, *Streptococcus lactis*, *Streptococcus agalacti*ae, *Bacillus thuringiensis*, *Listeria monocytogenes* and *Staphylococcus aureus*. The LAB can be transformed purposely with any foreign gene or DNA fragment which codes for the expression and secretion of an enzyme of interest (Toomey et al., 2009).

Secondly, transduction is the transfer of chromosomal or plasmid genetic information from donor to recipient bacteria by a bacteriophage (figure 2). It is a specific gene transfer event as bacteriophages are specialized viruses that infect certain bacteria (Lawrence, 2002). During a lytic cycle, the enzyme responsible for packaging phage DNA into the viral capsid sometimes accidentally packages fragment of host genome. In transduction the quantity of the transferred genetic material is limited by the phage capsid size. In the LAB phage-mediated gene exchange was for the first time reported by Sandine et al. (1962) who noticed transduction of triptophan biosynthesis and streptomycin resistance markers by a virulent *Lc. lactis* bacteriophage. The transduction in the LAB represented the first gene transfer technique used and developed for the transfer of technologically important traits between different LAB strains (Gasson and Shearman, 2003).

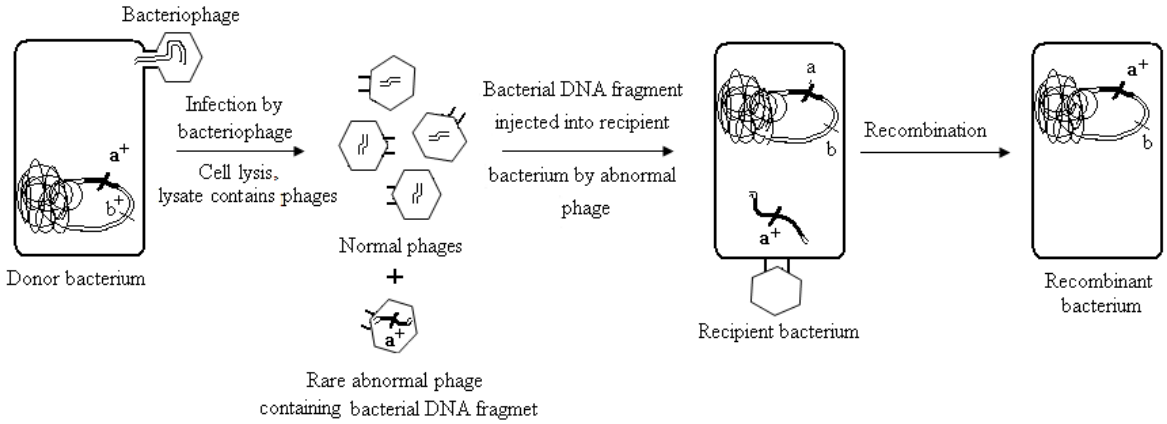

Figure 2: Schematic display of lactic acid bacteria transduction. Transduction is process in which bacterial genomic DNA is moved from donor bacterium to recipient by the certain bacteriophage. Lysis of donor bacterium is continued after bacteriophage infection. In the cell lysate, numerous normal and rare abnormal phages which contain the genome fragment of bacterium donor can be found. Continued infection of recipient bacterium by abnormal phage and after homologous recombination or after integration by bacteriophage integrase, could result in the recombinant cell. Scheme is modified from Tamarin (2002) and Zaneveld et al. (2008)

Slika 2: Shematski prikaz transdukcije u bakterija mliječne kiseline. Transdukcija je proces u kojem se pomoću određenih bakteriofaga prenese bakterijska genomska DNA molekula iz stanice davatelja u stanicu primatelja. Nakon infekcije bakteriofagom dolazi do lize bakterije davatelja. U lizatu stanice mogu se naći brojni normalni i rijetki neobični fagi koji sadržavaju dijelove genoma bakterije davatelja. Daljnjom infekcijom bakterije primatelja s neobičnim fagom te nakon homologne rekombinacije ili posredstvom integraze bakteriofaga može nastati rekombinantna stanica. Prilagođeno prema Tamarin (2002.) i Zaneveld et al. (2008.)

Thirdly, conjugative transfer is mediated by certain plasmids or integrative conjugative genetic elements with specific transfer genes from donor to recipient bacterium (figure 3.). Plasmids, conjugative transposons, regions of bacterial chromosomes, and integrative and conjugative elements all transfer DNA in this kind of HGT (Burrus et al., 2002). The recipient cell that has received a DNA from a donor bacterium is called a transconjugant. In LAB, conjugation is mediated by pheromone-induced cell aggregation. Stable mating formation in *Enterococcus faecalis* cells requires containing of conjugative plasmid pAD1 or pCF10 for pheromone induction (Trieu-Cuot et al., 1988). Many plasmids are not self-transmissible, but can be mobilized from one bacterium to another in the presence of additional self-transmissible plasmid, using its mobilization proteins (Haig and Kazazian, 2004). The maximal size of the transferred region depends on the process of the transfer. It is the highest for conjugation, which can support the transfer of chromosome-size segments. All products of conjugation can be identified by molecular, phenotypic or microscopic analysis. It is assumed that the majority of bacterial gene transfer events in the nature occur by conjugation. Numerous conjugative plasmids and transposons have been shown to have a broad host range including Gram-negative and Gram-positive bacteria. HGT via conjugative pathways has been extensively documented in *Lactobacillales* and appears to be important for niche-specific adaptation (Teuber et al., 2003). Signs of HGT are particularly notable in *Lc. lactis* subsp. *cremoris* SK11 that harbours a conjugative plasmid pSK11A, and several additional plasmids carrying genes related to the growth in milk (Siezen et al., 2005).

Evolution of lactic acid bacteria

Evolution of prokaryotes occurs constantly in nature through the selection of the most fitted population to its environment. Like all prokaryotes, the LAB are prone to gene exchange to increase the survival rate in harsh environment. As LAB are present in various biotopes, such as human and animal intestines or bovine rumen and udder, they are regularly exposed to different kinds of stress. Numerous phylogenetic analyses, comparison of gene content across the group and reconstruction of ancestral gene sets, evidence a combination of extensive gene loss and key gene acquisitions via HGT during coevolution of LAB within their habitats.

HGT via bacteriophage-mediated or conjugative pathways has been extensively documented in order *Lactobacillales* and appears to be important for niche-specific adaptation in the LAB (O'Sullivan et al., 2009). Consequently, in certain LAB biotopes there is no barrier to gene exchange between commensal, pathogenic and potentially pathogenic bacteria (Treuber et al., 2003). Conjugative transfer

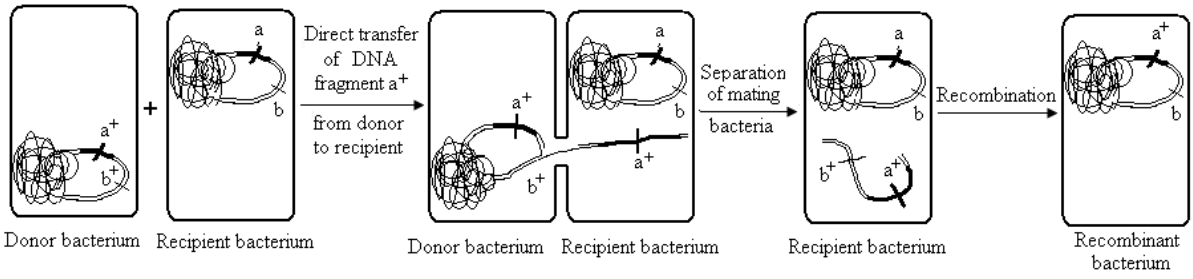

Figure 3: Schematic display of lactic acid bacteria conjugation. Conjugation is a process in which a part of genome (plasmid or part of chromosome) is transferred by a direct cytoplasmic contact of donor and recipient cells by direct cell-to-cell contact in pheromone-induced cell aggregation. Recombinant cell could result after homologous recombination. Scheme is modified from Tamarin (2002) and Zaneveld et al. (2008)

Slika 3: Shematski prikaz konjugacije u bakterija mliječne kiseline. Tijekom gomilanja stanica pod utjecajem feromona dolazi do neposrednog citoplazmatskog kontakta stanice davatelja koja predaje dio genoma (plazmid ili dio kromosoma) stanici primatelja. Homolognom rekombinacijom može nastati rekombinantna stanica. Prilagođeno prema Tamarin (2002.) i Zaneveld et al. (2008.)

of a self-transmissible plasmid from an engineered strain of *Lc. lactis* subspecies *lactis* IL 1403 to wild-type strains of *Lc. lactis* subspecies *lactis* and subspecies *cremoris* of technological interest occurred on solid surface mating that is, however, about 3 to 4 orders of magnitude lower during cheese manufacturing (Gabingauthier et al., 1991). An ecological niche suitable for the transfer between lactococci and enteric bacteria is the human and animal digestive tract. Gruzza et al., (1994) reported that conjugational gene transfer from *Lc. lactis* passed through the mouse digestive tract to the resident bacteria. Moreover, Bolotin et al. (2004) concluded that the genome sequence of *Lc. lactis* revealed that the *ycdB* gene was recently exchanged between lactococci and enterobacteria.

The genome sequences of *Lactobacillus johnsonii*, *Lactobacillus acidophilus* and *Lactobacillus delbrueckii* have recently become available (Pridmore et al., 2004; Altermann et al., 2005; van de Guchte et al., 2006) along with the genome sequences of *Lactobacillus plantarum* and *Lactobacillus sakei* (Kleerebezem et al., 2003; Chaillou et al., 2005), two more distantly related lactobacilli that do not belong to the acidophilus complex. These data have allowed a better understanding of the evolutionary relationship between the lactobacilli of the acidophilus complex. The results of van de Guchte et al., (2006) have shown that the similarly sized genomes in this group share a conserved structural backbone, evidenced by a clear global synteny (the two genes which occur on the same chromosome) and indicative of their close relatedness. Analysis of Nicolas et al. (2007), based on the rRNA and protein sequences based phylogeny methods, have revealed that extensive HGT takes place between the *L. acidophilus* and *L. johnsonii* species lineages, possibly in the gastrointestinal tract. Organisms that share ecological niches are more prone to exchange genes than organisms which do not share them (Kunin and Ouzounis, 2003).

Although the LAB occupy a diverse set of ecological niches such as fermenting milk, bread, plants, they are phylogenetically closely related by their small genomes and common metabolic pathways for sugar fermentation and lactic acid production (de Vos et al., 2005; Jamuna and Jeevaretnam, 2004; Aymerich et al., 2000). This suggests that a considerable ecological selection has occurred during their evolution (Kok et al., 2005). Pfeiler and Klaenhammer (2007) concluded that many of the LAB genomes have reduced biosynthetic capacities as a result of genome degradation events reflecting their adaptation to relatively nutrient-rich food environments, such as milk and the gastrointestinal tract. Finally, Makarova and Koonin (2007) have concluded that trends of gene loss are very similar in taxonomically distant LAB, particularly between *Lactobacillales* and *Bifidobacterium longum*, an actinomycete, conceivably due to similar environmental pressures.

The LAB plasmid profiles also contribute to characteristic trait of autochthonic dairy products. Among nine LAB genome sequences and their phylogenetic and functional analysis Makarova et al. (2006) presented data for *Lactobacillus brevis* ATCC 367 which harbors two plasmids, pLVIS1 and pLVIS2, of 13.413 and 35.595 kb in size, receptively. Comparison of this strain with *L. brevis* L62 from Stock cultures collection of Faculty of Food Technology and Biotechnology, University of Zagreb, showed different plasmid profiles. *L. brevis* L62 has three plasmids P1, P2 and P3, approximately of 25, 18 and 7 kb in size, receptively, with different restriction enzyme pattern than pLVIS1 and pLVIS2 (Butorac et al., 2008).

Traditional dairy products

Many reports of traditional dairy products have shown their characteristic and unique microflora dependence on the production technology as well as on the local ecological determinants. Some of reports are connected with LAB isolated from following dairy products: from the Camembert cheese (Corroler et al., 1998), from traditional Pecorino Sardo cheese (Mannu et al., 2000), from African traditional fermented milks (Beukes et al., 2001), from Kule naoto (Mathara et al., 2004), from Tetilla raw milk cheeses (Menéndez et al., 2004.), from fermented milk "laban" (Chammas et al., 2006), from Romanian dairy products (Zamfir et al., 2006), from Caciocavallo Pugliese cheese (Morea et al., 2007) from the Himalayan ethnic fermented milk products (Dewan and Tamang, 2007), from Batzos, a Greek PDO raw goat milk cheese (Pson et al., 2007), from Italian artisanal Raschera PDO cheese (Dolci et al., 2007), and many others. The

characterization and isolation of autochthonic LAB from dairy products are essential for understanding of their biochemical and microbiological properties that lead to the development of specific flavor and textures of traditional dairy products. Taken together, in the last two decades much effort has been put into the biochemical, genetic and technological characterization of the "wild" LAB strains isolated from traditional dairy products recognized as Protected Designation of Origin (Corroler et al., 1998; Gaya et al., 1999; Mannu et al., 2000; Sanchez et al., 2000; Mannu and Paba, 2002; Čanžek Majhenič et al., 2005; Psoni et al., 2007; Dolci et al., 2007), but also from others made with natural or no starter cultures (Cogan et al., 1997; Desmasures et al., 1998; Delgado and Mayo, 2004). Finally, the microbial composition of traditional dairy products, at genus and species level, is believed to be of great importance to the dairy industry (Fortina et al., 1998; Giraffa et al., 1998) as a source of genetic material, especially at present when expanding antibiotic resistance of LAB species is evident due to extensive antibiotic treatment in human and veterinary medicine as well as agriculture (Teuber, 2001; Mathur and Singh, 2005). Furthermore, new resistance can appear by at least three processes such as: mutation in targeting site, the advantaging of entire species, and by the escape of resistance genes to mobilome (Poole, 2002). There is now a concern that LAB in dairy products may act as reservoirs of antibiotic resistance genes (Mathur and Singh, 2005; Wang et al., 2006).

Conclusions

Up to date studies have shown growing diversity of the LAB in dairy products. The critical factors in the LAB evolution are the rearrangement of genetic material within the genome and the mobility of genes among strains and species in certain niche. As described in this review, the results of recent studies indicate a great possibility of gene acquisition due to horizontal gene transfer. To ensure the quality of industrial and autochthonous dairy products the microbiological, biochemical and chemical characterization of the LAB cultures is very important. Taking into account that there are various autochthonous dairy products coming from different counties in Croatia, it would be essential to describe and preserve autochthonous LAB strains, enabling more detailed studies of horizontal gene transfer, and mobilome activity in these local LAB populations.

Utjecaj prijenosa gena na evoluciju bakterija mliječne kiseline

Sažetak

Tijekom tisućljeća u cijelom su svijetu bakterije mliječne kiseline bile prijeko potrebne za pripremu raznovrsnih mliječnih proizvoda. Brojne usporedne analize sekvencija gena i genoma prokariota pokazuju da su izmjene genetičkoga materijala unutar i između bakterijskih vrsta mnogo uobičajenije i češće nego se prije mislilo. Stoga je horizontalni prijenos gena između udaljenih vrsta i unutar iste vrste osobito važan za evoluciju bakterija reda *Lactobacillales*. Radi dobrobiti za ljudsko zdravlje, izmjena genetičkih informacija tijekom horizontalnog prijenosa gena, pokretni genetički elementi i evolucija laktobacila vrlo su značajni zbog karakterizacije i očuvanja stabilnosti autohtonih, a i industrijskih sojeva bakterija mliječne kiseline u mliječnim proizvodima.

Ključne riječi: bakterije mliječne kiseline, horizontalni prijenos gena, pokretni genetički elementi, evolucija

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Acknowledgement

We would like to thank Jasenka Pigac for many helpful discussions and critical reading of the manuscript. This study was supported by a grant from the Ministry of Science, Education and Sport, Republic of Croatia, No.0583444-3446