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Review

Diversity and safety hazards of bacteria involved in meat fermentations

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ABSTRACT

Food safety is a major concern for consumers and a major issue for industry which has become aware of the importance of the starter safety assessment. In the European Union, the Food Safety Authority has introduced the Qualified Presumption of Safety (QPS) approach for safety assessment of microorganisms throughout the food chain. This assessment relies on: taxonomy, familiarity, pathogenicity and end use. Productions of toxins as well as biogenic amines by food isolates are both of major concern as they can lead to food poisoning. The other important criterion is the presence of transmissible antibiotic resistance markers. This review underlined that the main hazard of bacteria involved in food fermentations concerns antibiotic resistance and particularly the presence of transferable genetic determinants that may present a risk for public health. Selection of starter strains should consider this hazard. Following the QPS approach, a list of bacteria has been acknowledged acceptable for consumption.

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1. Introduction

The technology for producing fermented foods has been known since ancient times in most parts of the world. Originally the fermentation of these foods only relied on indigenous microbiota but the inoculation of microorganisms has been applied for the past 100 years. The extensive use of starter cultures dates back to the middle of the 20th century. In fermented meat products, pasteurisation of raw materials is not desirable, thus fermentation relies either only on “house flora” for traditional products or on starter cultures for artisanal and industrial sausages which must be competitive to prevent outgrowth of indigenous bacteria (Leroy, Verluyten, & De Vuyst, 2006).

Food safety is still a major concern for consumers and a major issue for industry which has become aware of the importance of the starter safety assessment. In contrast to the European Union (EU) regulation on microorganisms entering the food chain in association with animal feeds or as plant protection products, there are no recognised means for microorganisms to be formally considered safe when used for human food preparation. The widely known standard is the GRAS status (Generally Recognised as safe) from the US Food Drug Administration (FDA) which has a list of microorganisms considered safe for a specific use (Chamba & Jamet, 2008). In the EU, a similar approach has been proposed by the European Food Safety Authority (EFSA, Regulation (EC) n° 178/2002). This authority has introduced the Qualified Presumption of Safety (QPS) approach for safety assessment of microorganisms throughout the food chain (EFSA, 2004). The safety assessment relies on four pillars: taxonomy, familiarity, pathogenicity and end use (EFSA, 2005a). The term ‘familiarity’ or ‘body of knowledge’ includes history of use, ecology,

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industrial applications and scientific literature. The degree of familiarity is obviously higher for microorganisms widely used for several decades. The International Dairy Federation (IDF) in collaboration with the European Food and Feed Cultures Association (EFFCA) has listed the microorganisms with a documented history of use in human food at international level (Mogensen et al., 2002). The EFSA has also established a list of microorganisms proposed for QPS status (EFSA, 2004).

2. Inventory of bacteria with a history of use in meat products

The first step in the QPS assessment is to establish the precise identity of the microorganism at genus and species levels and if relevant at the subspecies and strain levels.

In meat fermentation two main groups of bacteria are considered important: the lactic acid bacteria (LAB) and the coagulase-negative staphylococci (CNS). The initial population of LAB is usually low in the raw material (3 to 4 log CFU/g) but it becomes dominant during the fermentation step (8 log CFU/g) in traditional sausages (Comi et al., 2005; Greco, Mazette, De Santis, Corona, & Cosseddu 2005; Lebert et al. 2007). LAB contribute to sausage sensorial properties mainly through their acidification (Leroy et al., 2006). The development of a functional microarray dedicated to LAB and targeting genes that play key roles in sugar catabolism, in the production of bacteriocins, exopolysaccharides and flavour will allow characterising the LAB dynamics in complex sausage ecosystems (Weckx et al., 2009). CNS frequently represent the second population varying from 5 to 7 log CFU/g in traditional sausages (Blaiotta et al. 2004b; Corbière Morot-Bizot, Leroy, & Talon 2006; Iacumin, Comi, Cantoni, & Cocolin 2006; Mauriello, Casaburi, Blaiotta, & Villani 2004). They participate to the development and stability of the colour and contribute to the flavour through their antioxidant properties and amino acid catabolism (F. Leroy et al., 2006; Talon, Leroy-Sétrin, & Fadda 2002). Similarly, the development of a DNA microarray for CNS targeting genes involved in technological properties such as the ones coding for proteases, lipases, nitrate dissimilation, catalase and superoxide dismutase will allow to characterise their expression *in situ* in sausages (Seitter, Nerz, Rosenstein, Götz, & Hertel 2011).

In the last decade, the development of molecular methods has allowed reliable identification of staphylococci (Aymerich, Martin, Garriga, & Hugas 2003; Corbière Morot-Bizot, Talon, & Leroy 2004; Giammarinaro, Leroy, Chacornac, Delmas, & Talon 2005) and LAB (Aymerich et al., 2006; Rantsiou et al., 2005). Moreover, combining the study of the microbial ecology by culture-dependent and -independent methods has contributed to a better understanding of microbial dynamics during sausage manufacturing (Rantsiou & Cocolin, 2006).

The main LAB genera isolated from fermented dry sausages are *Lactobacillus*, *Pediococcus*, *Leuconostoc*, *Weissella* and *Enterococcus* (Albano et al., 2009; Ammor & Mayo, 2007). Usually *Lactobacillus* species are dominant in sausages, however in some slightly acidified sausages from southern Europe, *Enterococcus* and *Lactobacillus* species cohabit (Lebert et al., 2007; Martin, Garriga, Hugas, & Aymerich 2005). Among lactobacilli, *Lactobacillus sakei*, *Lactobacillus curvatus* and/or *Lactobacillus plantarum* generally constitute the predominant microbiota during traditional sausage ripening (Bonomo, Ricciardi, Zotta, Parente, & Salzano 2008; Cocolin et al., 2009; Lebert et al., 2007; Silvestri et al., 2007). Other lactobacilli that may be found at minor levels include *Lactobacillus pentosus*, *Lactobacillus paracasei*, *Lactobacillus casei* and *Lactobacillus alimentarius* (Aymerich et al., 2006; Comi et al., 2005; Greco et al., 2005; Papamanoli, Tzanetakis, Litopoulou-Tzanetaki, & Kotzekidou 2003; Rantsiou et al., 2005). *Enterococcus faecium* and *Enterococcus faecalis* were the most frequently isolated species from two slightly fermented Spanish sausages (Martin et al., 2005). *Pediococci* are less frequently isolated from European sausages except from Iberian dry fermented sausages and Chorizo (Benito et al.,

2007; Benito et al., 2008) and certain Italian sausages (Bonomo et al., 2008). They are more common in fermented sausages from the United States where *Pediococcus acidilactici* and *Pediococcus pentosaceus* are added as starter cultures (F. Leroy et al., 2006). In the EU, *L. sakei*, *L. curvatus*, *L. plantarum* and *L. pentosus* are the species most commonly used as starter culture in sausage manufacturing (Ammor & Mayo, 2007; Talon et al., 2002). A high biodiversity at strain level inside the predominant species has been reported. The clustering analysis of 295 LAB isolates from different kinds of sausages produced in Hungary, Italy, and Greece gave 5 different clusters for the 27 isolates of *L. plantarum*, 9 clusters for the 100 isolates of *L. curvatus* and 19 clusters for the 168 isolates of *L. sakei* (Rantsiou et al., 2005). Aymerich et al. (2006) were able to distinguish 144 different RAPD/plasmid profiles among 250 LAB isolates from 21 different Spanish slightly fermented sausages with *L. sakei* showing 112 different strains out of 185 isolates. An intraspecies diversity among 73 isolates of *L. sakei* sourced from different countries was determined using a PCR-based method that detects the possession of 60 chromosomal genes belonging to the flexible gene pool. Ten different strain clusters were identified and many different genotypes may be isolated from similar types of meat products, suggesting a complex ecological habitat in which intraspecies diversity may be required for successful adaptation (Chaillou et al., 2009).

The species used as starter cultures belonging to the *Lactobacillus* and *Pediococcus* genera have a long history of apparent safe use in industrial meat applications. Some species are also used in a variety of food fermentation such as dairy products (*P. acidilactici*), fermented vegetables, sourdough and silage (*L. plantarum*) (Mogensen et al., 2002). Moreover and as mentioned above, some species are among the dominant population in microbial communities of traditional fermented sausages, being part of the natural starter cultures. Unlike the two genera mentioned above, the enterococci have the paradoxical position of being considered positive for meat and dairy fermentation but also constitute a potential risk (Hugas, Garriga, & Aymerich 2003; Ogier & Serrero, 2008). Thus numerous attempts have been done to type the isolates of *E. faecalis* and *E. faecium* from different origins. The strains typing of 106 enterococci isolates from fermented sausages revealed that 60 strains exhibited different RAPD profiles indicating a high genetic variability (Martin et al., 2005). Pulse field gel electrophoresis (PFGE) analysis has been successfully used to differentiate between clinical and food isolates of *E. faecalis* and *E. faecium* (Ogier & Serrero, 2008). Multilocus sequence typing and multilocus variable analyses applied to 411 isolates of *E. faecium* from different continents and ecological niches have revealed that most of derived vancomycin-resistant enterococci are part of a single clonal lineage (Willems et al., 2005). In spite of the wide range of molecular typing it remains difficult to clearly differentiate food and clinical isolates.

The staphylococcal ecosystem of traditional dry fermented sausages is diverse with many species cohabiting. However, *Staphylococcus xylosum*, *Staphylococcus equorum* and *Staphylococcus saprophyticus* are the three prevalent species (Bonomo, Ricciardi, Zotta, Sico, & Salzano 2009; Cocolin, Manzano, Aggio, Cantoni, & Comi 2001; Coton et al., 2010; Mauriello et al., 2004; Leroy, Giammarinaro, Chacornac, Lebert, & Talon 2010). A wide diversity among minor species could be found, e.g. up to 15 species identified in French traditional sausages (S. Leroy et al., 2010) but *Staphylococcus succinus*, *Staphylococcus carnosus*, *Staphylococcus warneri* and *Staphylococcus epidermidis* are frequently reported (Aymerich et al., 2003; Corbière Morot-Bizot et al., 2006). Among CNS, only *S. carnosus* and *S. xylosum* species are used as starter cultures for manufacturing dry sausages in the EU (Corbière Morot-Bizot, Leroy, & Talon 2007). The natural habitat of CNS is the skin and the mucous membranes of animals and humans (Irlinger, 2008). Foods constitute a man-made habitat in which intentionally added and naturally occurring CNS may grow and modify their sensorial characteristics. CNS are isolated from a wide

range of foods from animal origin such as meat and meat products, milk and cheese (Blaiotta et al. 2004b; Irlinger, 2008; S. Leroy et al., 2010; Martín et al., 2006). It is noteworthy that the three prevalent species in fermented sausages, *S. xylosum*, *S. equorum* and *S. saprophyticus*, were also frequently isolated from various cheeses (Coton et al., 2010).

The infraspecies of food CNS have been characterised and high genetic diversity was revealed by PFGE analysis of isolates from cheeses and meat products of *S. saprophyticus*, *S. equorum* and *S. xylosum* (Coton et al., 2010, S. Leroy et al., 2009; Rossi, Tofalo, Torriani, & Suzzi 2001; Villard et al., 2003). For example, the diversity of strains of *S. equorum* isolated from traditional French sausages and their manufacturing environments have been highlighted with 52 profiles for 118 isolates and 28 profiles for 71 isolates (S. Leroy et al., 2009, S. Leroy et al., 2010). Moreover these two studies revealed that the diversity was maintained throughout the process. As some species found in food could be involved in human or animal infections, comparison of PFGE profiles has been carried out. High genetic diversity was revealed and no common profile was found between isolates from food and clinical samples of *S. saprophyticus* and *S. epidermidis* (Coton et al., 2010). *S. xylosum* strains of food and mastitis origins were genetically clearly distinct (Dordet-Frisoni, Dorchies, De Araujo, Talon, & Leroy 2007).

3. Are there safety concerns for meat-associated lactic acid bacteria and coagulase negative staphylococci?

Lactobacilli and pediococci have generally been considered to be non-pathogenic. Species of these genera have been occasionally encountered in clinical specimens usually affecting immunocompromised patients (Bernardeau, Vernoux, Henri-Dubernet, & Gueguen 2008).

Enterococci have been involved in nosocomial infections, in particular *E. faecalis* and *E. faecium*, two species commonly isolated from food products and in fermented meats (Ogier & Serror 2008). For CNS, *S. xylosum* and *S. equorum* two dominant species in meat products have rarely been associated with clinical cases (Irlinger, 2008; Novakova et al., 2006). *S. saprophyticus* frequently isolated from meat products is associated with urinary tract infections (Piette & Verschraegen, 2009) and *S. epidermidis* episodically isolated is associated with nosocomial infections (Stevens et al., 2008).

It is worth noting that CNS and enterococci species associated with clinical cases have not been reported to be associated with food consumption (Irlinger, 2008; Ogier & Serror, 2008). However, the occurrence and the pathogenic potential of some species including species isolated from food reinforce the need to assess the safety of the food isolates.

In the food context, productions of toxins as well as biogenic amines by food isolates are both of major concern as they can lead to food poisoning. The other important criterion in the evaluation of strain safety is the presence of transmissible antibiotic resistance markers.

DNA microarrays have been developed to characterise these safety hazards. For CNS, two microarrays have been developed, one with 268 genes targeting only safety hazards (Even et al., 2010), and the other with 220 genes targeting safety hazards and technological properties (Seitter et al., 2011). Similarly a functional microarray dedicated to LAB has been developed to screen safety hazards in particular antibiotic resistance (Weckx et al., 2009).

3.1. Toxin production

Staphylococcal intoxication worldwide stands out as one of the main food-borne diseases. For many years, staphylococcal food poisoning was uniquely associated with coagulase positive *Staphylococcus aureus* and its production of staphylococcal enterotoxins (SEs).

Nine major antigenic types of SEs have been reported: the classical five SEA to SEE and the four additional SEG to SEJ (Blaiotta et al. 2004a; Le Loir, Baron, & Gautier 2003). Detection of nine additional genes (*seK* to *seR* and *seU*) coding homologous enterotoxins expanded the SE family (Blaiotta et al. 2004a). Furthermore for SEC, SEG, SEI and SEU several variants were also reported. No relationship between these new SEs and human food poisoning has been described as yet.

Staphylococcal enterotoxins have been studied in CNS isolated from food. Recent studies either by PCR and/or DNA microarrays revealed that the occurrence of SEs genes in CNS isolated from meat products, milk and cheeses was very rare. No enterotoxins genes were detected in large collections of 87 and 128 CNS strains of *S. equorum*, *S. xylosum* and *S. saprophyticus* (Blaiotta et al. 2004a; Even et al., 2010). Similarly, no SE genes were found in 32 CNS strains including *S. equorum*, *S. xylosum* and *S. carnosus* species (Seitter et al., 2011). By PCR and immunoassay, Rosec, Guiraud, Dalet, and Richard (1997) showed that 51 CNS strains isolated from various foods did not produce enterotoxins SEA to SEE. These results contrast with previous works pointing out CNS strains that produce enterotoxins. In particular, seven out of the 32 strains studied by Seitter et al. (2011) have been shown to produce enterotoxins by immunoblot analysis, with SED and SEH being the most commonly produced, mainly by *S. equorum* strains (Zell et al., 2008). By immunoassay, few strains of CNS isolated from dry cured Spanish ham were able to produce enterotoxin C and/or D: one *S. xylosum*, one *S. cohnii* and one *S. epidermidis* (Rodríguez, Nunez, Cordoba, Bermudez, & Asensio 1996). Still by immunoassay, few CNS, identified at the species level by phenotypic methods, isolated from sheep milk or from goat milk and cheese were shown to produce classical enterotoxins (Bautista, Gaya, Medina, & Nunez 1988; Vernozy-Rozand et al., 1996).

Enterotoxigenic capacity of CNS has always been a subject of controversy. Methods used for screening might account for discrepancies between results relying on detection of SE production by immunological methods and results based on the presence of the corresponding genes. Immunoassays to detect enterotoxins have been reported to lead false diagnoses due to interferences, lack of specificity and/or sensitivity (Dupuis, Hennekinne, Garin, & Brun 2008). In accordance, SE detection based on immunological approaches is not always confirmed by DNA-based tests and vice versa (Rodríguez et al., 1996; Seitter et al., 2011; Zell et al., 2008). Besides, one cannot exclude the existence of enterotoxin gene variants (diverging from *S. aureus* sequences) in CNS species (although no such variant has been described so far), which are not detected by microarrays or by PCR. However, no case of food poisoning involving exclusively strains of CNS of food origin has been reported so far.

Further investigation of the toxigenic potential of CNS revealed that haemolytic activity could be detected. From a collection of 330 CNS isolated from food including fermented and cured meats and meat starter cultures, 59% of the strains exhibited weak to moderate haemolytic activity with human blood (Zell et al., 2008) but only weak hybridization signals were obtained with 3 strains for *hly* gene coding δ -hemolysin (Seitter et al., 2011). Presence of *hly* gene was detected in 5 strains by microarrays but only one *S. epidermidis* was confirmed by PCR (Even et al., 2010).

In conclusion, food related CNS exhibit low toxigenic and enterotoxigenic potential. Acquisition by CNS strains of genes encoding toxins from *S. aureus* or other Gram-positive bacteria sharing the same ecosystem appeared to be very limited (Even et al., 2010), even if some of these toxins, especially enterotoxins, are carried by mobile genetic elements (Baba et al., 2002).

3.2. Biogenic amine production

Among food safety hazards associated with LAB and CNS, the potential production of biogenic amines has to be considered. Biogenic amines are generated in various fermented foods through

bacterial amino acid decarboxylation. Cadaverine, histamine, putrescine, tryptamine, tyramine and phenylethylamine are regarded as undesirable because of their toxic effects. From a toxicological aspect, the vasoactive and psychoactive effects of amines are related to the occurrence of histaminic intoxication, food-induced migraines and hypertensive crises in sensitive individuals (Suzzi & Gardini, 2003). In such people, the action of amine oxidases, the enzymes involved in the detoxification of these substances are deficient (Suzzi & Gardini, 2003). A regulation is already in force in the fish industry in EU and may be extended to fermented food in the future.

The content of biogenic amines can be relatively high in fermented food, especially in raw materials (meat and dairy products) presenting a high content of proteins combined with high proteolytic activity (Suzzi & Gardini, 2003). Such a situation is met in dry sausages where many studies reported variable level of amines (Ansorena et al., 2002; Latorre-Moratalla et al., 2008). A lot of information concerns the production of biogenic amines by LAB. Some LAB (48%) isolated from dry fermented sausages decarboxylated one or more amino acids (Latorre-Moratalla et al., 2010). Aminogenic potential is species and strain dependent. Most *L. curvatus*, *E. faecium* and *E. faecalis* strains isolated from dry fermented sausages produced tyramine and phenylethylamine whereas all the *L. sakei* strains were nonaminogenic (Aymerich et al., 2006; Bover-Cid, Hugas, Izquierdo-Pulido, & Vidal-Carou 2001; Hugas et al. 2003; Latorre-Moratalla et al., 2010). Enterococci isolated from cheese have been described as tyramine and tryptamine producers and production of biogenic amines in milk has also been observed (Garg & Mital, 1991).

By comparison, biogenic amine production by CNS in fermented products is poorly documented. It has never been described in dairy products and only few studies reported their production by CNS isolated from meat products (Martín et al., 2006). The percentage of CNS able to produce detectable amounts of biogenic amines is low and varied from 6% to 14% (Even et al., 2010; Latorre-Moratalla et al., 2010; Martín et al., 2006). The described aminogenic strains belong to *S. xylosum*, *S. warneri*, *S. epidermidis* and *S. carnosus*. Phenylethylamine was the amine the most frequently produced followed by tyramine (Martín et al., 2006).

In conclusion, selection of LAB and to a lesser extent of CNS, to be used as starter cultures for sausage production should consider the criteria of absence of amino decarboxylase activity.

3.3. Antibiotic resistance

Antibioresistance of food bacteria has aroused great interest because they may act as reservoirs for antibiotic resistance genes. Fermented foods may be important vehicles of high amounts of living bacteria into the human body. They may carry transferable antibiotic resistances, which might be transferred to commensal or pathogenic bacteria. Therefore, the presence of transmissible antibiotic resistance genes in the evaluation of strains is an important safety criterion.

Antibiotic resistance trends among *E. faecalis* and *E. faecium* have been extensively investigated, in particular in clinical and human isolates. *E. faecium* clinical isolates are intrinsically resistant to penicillin and have acquired genetic determinants conferring resistance to glycopeptides (vancomycin, teicoplanin) and to synergic action of β -lactams and aminoglycosides (Ogier & Serror, 2008). Although antibiotic resistant enterococci are isolated from foods, only few are resistant to clinically important antibiotics ampicillin, penicillin, gentamicin and vancomycin (Martín et al., 2006; Ogier & Serror, 2008).

Resistance to rifampicin, ciprofloxacin and erythromycin was observed in most *E. faecalis* and *E. faecium* strains isolated from fermented sausages. Furthermore, *E. faecalis* strains were resistant to chloramphenicol (93%) and tetracycline (87%), whereas *E. faecium* strains showed higher incidence of penicillin and ampicillin resistances (Martín et al., 2006). Resistances to chloramphenicol,

erythromycin and tetracycline were already noticed for dairy *E. faecalis* isolates (Teuber, Meile, & Schwarz 1999). The frequent detection of antibiotic resistance among food enterococci is probably due to the efficient transfer mechanisms of resistance genes via conjugative plasmids and transposons. For example tetracycline resistance (*Tet*^r) is one of the most commonly acquired forms of antibiotic resistance in food enterococci isolates. Huys, D'Haene, Collard, and Swings (2004) showed that *Tet*^r in food enterococci is mainly conferred by the same *tet* determinants (*tetM*, *tetL*, *tetS*) as those previously found in clinical and veterinary isolates. These authors showed also that a significant proportion of *Tet*^r isolates exhibited co-resistance to erythromycin and/or chloramphenicol suggesting that *Tet*^r genes are associated with transposons carrying multiple antibioresistance genes (Huys et al., 2004). During the past years, several studies have reported antibiotic resistance gene transfers i) in laboratory conditions between clinical, commensal, food and probiotic isolates (Lund & Edlund, 2001), ii) in food matrix : cheese and sausage (Cocconcelli, Cattivelli, & Gazzola 2003) and iii) in gnotobiotic mice (Moubareck, Bourgeois, Courvalin, & Doucet-Populaire 2003). Recently, a transfer of *vanA* gene has been showed between *Enterococcus* strains in the digestive tract of mice colonised by human microbiota (Mater, Langella, Corthier, & Flores 2005). The transfer of resistance gene from *E. faecalis* to pathogenic species has been demonstrated for *S. aureus* in a cutaneous mouse model and *Listeria monocytogenes* *in vitro* (Biavasco et al., 1996). Moreover, gene transfer has been implicated in the emergence of vancomycin- and methicillin-resistant *S. aureus* (Tenover & McDonald, 2005).

Generally, LAB belonging to the genera *Lactobacillus*, *Streptococcus*, *Lactococcus*, *Pediococcus* and *Leuconostoc* have a high natural resistance to ciprofloxacin, gentamicin and streptomycin indicating that these may constitute intrinsic resistance (Table 1). LAB are generally sensitive to erythromycin, chloramphenicol, tetracycline or β -lactams (Aymerich et al., 2006; Hummel, Hertel, Holzapfel, & Franz 2007). All *L. sakei* and *L. curvatus* meat strains were resistant to vancomycin (Aymerich et al., 2006) (Table 1). Such resistance was also described for *L. plantarum*, *L. casei*, *L. salivarius* and *L. acidophilus* that have intrinsic resistance to this drug (Bernardeau et al. 2008). However, some data highlighted the presence of transferable antibioresistance genes. Tetracycline resistance gene, in particular *tetM*, localised in a plasmid has been identified in *L. sakei*, *L. alimentarius* and *L. plantarum* strains isolated from fermented sausages (Gevers et al., 2003) and *tetM* residing in a plasmid was found in *Lactobacillus reuteri* and *Bifidobacterium lactis*, two probiotic cultures (Kastner et al., 2006). Recently, strains belonging to *L. sakei*, *L. curvatus* and *L. plantarum* isolated from Italian fermented sausages were found resistant to tetracycline with *tetM* gene most frequently detected but *tetW* was also detected (Table 1) (Zonenschain, Rebecchi, & Morelli 2009). The *tetM* gene can also be linked to a family of transposons known for its ability to perform conjugative transposition with direct transfer between different bacteria (Sorum & L'Abée-Lund, 2002). These strains were also resistant to erythromycin mainly associated to the presence of the *ermB* gene (Table 1) (Zonenschain et al., 2009).

The most frequent resistances found in CNS of food origin were those to ampicillin, erythromycin, penicillin, lincomycin and tetracycline (Table 2). The incidence of resistance in food CNS varied strongly between strains, ranging from a complete lack of resistance (56%) to resistance up six antibiotics: 2.3% of strains for Even et al. (2010) and 7% of strains for Resch, Nagel, and Hertel (2008). Multi-resistance of CNS isolated from meat or sausage has been also reported by Mauriello, Moschetti, Villani, Blaiotta, and Coppola (2000) and Simeoni et al. (2008). The incidence of antibiotic resistance was also found to be species-dependent: resistance to at least one antibiotic was observed in 36% and 26% of *S. xylosum* and *S. equorum* strains, respectively (Even et al., 2010). Resch et al. (2008) found 12% of *S. carnosus*, 63% of *S. equorum* and 95% of *S. xylosum* resistant to

Table 1

Prevalence of antibiotic resistance in food-associated LAB (except enterococci).

Main species (number of strains)	Origin	Main antibiotic resistance (%)	Antibiotic-resistant genes (%)	Reference
<i>Lactobacillus</i> , <i>Streptococcus</i> , <i>Lactococcus</i> , <i>Pediococcus</i> , <i>Leuconostoc</i> (40)	Fermented sausage, cheese, yogurt	Gentamicin (71) Streptomycin (73) Ciprofloxacin (78) Tetracycline (100)		Hummel et al.(2007)
<i>L. curvatus</i> (3), <i>L. alimentarius</i> (3), <i>L. plantarum</i> (8), <i>L. sakei</i> (10) <i>L. curvatus</i> (53)	Fermented sausage		<i>tetM</i> (100)	Gevers et al. (2003)
	Fermented sausage	Gentamicin (100) Vancomycin (100) Ampicillin (15) Penicillin (11) Tetracycline (13)	ND	Aymerich et al.(2006)
<i>L. curvatus</i> (16)	Fermented sausage	Tetracycline (62) Erythromycin (62)	<i>tetM</i> (70), <i>tetW</i> (40) <i>ermB</i> (100)	Zonenschain et al.(2009)
<i>L. plantarum</i> (12)	Fermented sausage	Tetracycline (92) Erythromycin (50)	<i>tetM</i> (45), <i>tetW</i> (36), <i>tetS</i> (9) <i>ermB</i> (50), <i>ermC</i> (33)	Zonenschain et al.(2009)
<i>L. sakei</i> (185)	Fermented sausage	Gentamicin (100) Vancomycin (100) Ampicillin (52) Penicillin (33) Tetracycline (11)	ND	Aymerich et al.(2006)
<i>L. sakei</i> (24)	Fermented sausage	Tetracycline (71) Erythromycin (29)	<i>tetM</i> (64), <i>tetW</i> (9) <i>ermB</i> (71)	Zonenschain et al.(2009)
<i>L. mesenteroides</i> (12)	Fermented sausage	Gentamicin (67) Vancomycin (100) Ampicillin (42) Penicillin (50) Tetracycline (25)	ND	Aymerich et al.(2006)

ND: not done.

antibiotics. Comparison of the antibiotic resistance profiles established by phenotypic approach with either microarray or PCR data enabled assigning genes putatively involved in most antibiotic resistances. In most studies, resistances to penicillin, tetracycline, lincomycin and erythromycin were traced back to the presence of genes *blaZ*, *tetK* but also *tetM*, *lnuA*, *ermB* and *ermC* (Table 2). Normally *bla* genes coding β -lactamases are in transposons located on small

transferable or mobilisable plasmids (Sorum & L'Abée-Lund, 2002). The high incidence of *tetK* and *tetM* genes can be explained as mentioned above by their location on small multicopy plasmids and on conjugative transposons, respectively, which contribute to the spread of these determinants. Similarly, *ermC* gene is located on small multicopy plasmids while *ermB* is often carried by conjugative transposons, these locations explaining their spread (Simeoni et al.,

Table 2

Prevalence of antibiotic resistance in food-associated CNS.

Main species (number of strains)	Origin	Main antibiotic resistance (%)	Antibiotic-resistant genes (%)	Reference
<i>S. carnosus</i> (11)	Fermented sausage	Ampicillin (100) Penicillin (27)	ND	Martin et al.(2005)
<i>S. carnosus</i> (106)	Meat starter culture, fermented fish	Lincomycin (6)	None	Resch et al.(2008)
<i>S. equorum</i> (64)	Cured ham, fermented sausage, hard and soft cheese	Lincomycin (48), Oxacillin (19)	None	Resch et al.(2008)
<i>S. equorum</i> (31)	Fermented sausage, cheese	Erythromycin (20) Tetracycline (10)	None <i>tetK</i> (100)	Even et al.(2010)
<i>S. xylosum</i> (30)	Fermented sausage	Penicillin (90) Erythromycin (30) Lincomycin (93) Fusidic acid (73) Tetracycline (20)	ND	Mauriello et al. (2000)
<i>S. xylosum</i> (194)	Fermented sausage	Penicillin (82) Ampicillin (69) Erythromycin (36)	ND	Martin et al. (2005)
<i>S. xylosum</i> (33)	Fermented sausage	Penicillin (9) Nalidixic acid (9) Tetracycline (12)	None None <i>tetK</i> (100)	Kastner et al.(2006)
<i>S. xylosum</i> (137)	Meat starter culture, fermented sausage, cured ham, hard and soft cheese milk	Penicillin (69), Oxacillin (41), Ampicillin (48) Lincomycin (53), Fusidic acid (50), Tetracycline (36)	<i>blaZ</i> (10) <i>lnuA</i> (2)	Resch et al.(2008)
<i>S. xylosum</i> (12)	Pig feedstuff, meat, fermented sausage	Tetracycline Erythromycin Penicillin	<i>tetK</i> (100) <i>tetK</i> (67), <i>tetM</i> (50), <i>ermB</i> (83), <i>ermC</i> (41) <i>blaZ</i> (33)	Simeoni et al., 2008
<i>S. xylosum</i> (28)	Fermented sausage, cheese	Penicillin (32) Tetracycline (17)	<i>blaZ</i> (100) <i>tetK</i> (100)	Even et al.(2010)

ND: not done; none: resistance gene not found.

2008). However discrepancies between phenotypic antibiotic resistance and molecular determinant have often been reported (Even et al., 2010; Hummel et al., 2007; Seitter et al., 2011). Some genes may be present as pseudogenes but also some antibiotic resistances are due to complex intrinsic features such as cell wall structure or metabolic properties (Kastner et al., 2006). They may also be related to point mutations as for macrolide, quinolone, rifampicin and fusidic acid resistances (Even et al., 2010).

From this review, it appears that most antibiotic resistances are shared by the different food bacteria. The sequencing of several antibiotic resistance genes and of the genetic vectors responsible for mobility (transposons, plasmids) showed identity in their sequences independently of the origin of the strains (Sorum & L'Abée-Lund, 2002). Bacteria isolated from animals carrying antibiotic resistance genes could contaminate food of animal origin and could transfer their resistance to food and then human microbiota (Sorum & L'Abée-Lund, 2002). Modern industrialised food production adds extra emphasis on lowering the use of antibiotics in rearing domestic animals.

4. QPS status or not?

As underlined in this review, the main hazard of bacteria involved in food fermentation concerns antibiotic resistance. However and as adopted by EFSA (2005b), intrinsic resistance and resistance due to mutation of chromosomal genes present low risk of horizontal dissemination and such strains should be acceptable for consumption. While acquired resistance by mobile elements may present a risk for public health, safety assessment of starter strains should focus on antibiotic profile and transferable genetic determinants. The QPS status has been proposed for 32 selected species of *Lactobacillus* including the main species either found in naturally fermented sausages or added as starter cultures in meat products (EFSA, 2005a, 2005b). Regarding *Pediococcus*, *P. acidilactici* and *P. pentosaceus* used as starter culture are proposed for QPS status. Similarly, *S. xylosus* and *S. carnosus* used as starter culture are proposed for QPS status. While the *Enterococcus* genus is not proposed for the QPS status and a case-by-case evaluation of the potential of starter bacterial strain should be adopted.

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