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Original research

Characterisation of a new transferable MDR plasmid carrying the *pbp5* gene from a clade B commensal *Enterococcus faecium*

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Running title:

Transferable MDR plasmid carrying *pbp*5 gene in *E. faecium*

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Keywords: *Enterococcus faecium*, *Listeria welshimeri*, MDR plasmid, *pbp5* gene, clade B enterococci

Synopsis

Objectives: The aim of this work was to evaluate the transferability of antibiotic resistance from an MDR clade B *Enterococcus faecium* and to characterise the genetic elements involved.

Methods: The *erm*(B)-positive strain *E. faecium* 37BA (donor) and strains *E. faecium* 64/3 and *Listeria welshimeri* 11857RF (recipients) were used in mating experiments. Donor and transconjugants were characterised using MIC assays, PFGE, Southern blotting and hybridisation, RT-qPCR, NGS, and PCR mapping.

Results: One *E. faecium* and one *L. welshimeri* transconjugant were selected for in-depth investigation. Both acquired a ~40 kb plasmid carrying *erm*(B). An additional plasmid of ~200 kb, encoding a full conjugative machinery, was detected in the donor and in the *E. faecium* transconjugant. NGS disclosed a new 40,396 bp plasmid that was designated pEf37BA; it contained ten antibiotic resistance genes, *tet*(M), *tet*(L), *erm*(B), *aadE, sat4, aphA, spw, lsa*(E), *lnu*(B), and *pbp5* resulting from the recombination of pM7M2 of *E. faecium* with an MDR chromosomal region of *Erysipelothrix rhusiopathiae*. A *pbp5*-carrying circular form was also detected. The PBP5 amino acid sequence differed from the C46 variant by two mutations (S39T and D644N). Its expression was documented in both transconjugants. pEf37BA persisted in the absence of selective pressure.

Conclusions: The MDR clade B *E. faecium* plasmid, deriving from the recombination of two different resistance regions, carried a *pbp5* element and was transferable to different bacterial species. This finding further documents the dissemination of ampicillin resistance among community-associated *E. faecium* and the key role of commensal strains in the spread of antibiotic resistance.

Introduction

It is well established that the gut microbiota plays a crucial role in host health.[1] Several factors, including dietary habits and antibiotic use, contribute to shaping the normal gut microbiota in humans.[2] In particular, antibiotic therapy may affect their composition as well as the long-term persistence of resistant bacteria in the human gut.[3, 4] A variety of studies have documented an increase in antibiotic-resistant commensal bacteria, which provide a reservoir of antibiotic resistance (AR) genes that have the ability to spread to other gut bacterial species and genera, either resident or transient, including human pathogens.[4, 5] Among human gut commensals, enterococci have a striking ability to colonise healthy carriers and hospitalised patients and to adapt to adverse environmental conditions – including those created by drug administration – by virtue of their intrinsic resistance to a wide range of antimicrobial agents and of the plasticity of their genome, which favours the acquisition of AR traits.[6, 7] After acquiring multiple genetic elements, multidrug-resistant (MDR) enterococcal subpopulations easily disseminate from the gastrointestinal tract of patients and healthcare workers to the hospital environment, contributing to hospital-associated infections.[8, 9]

In 2016, enterococci ranked second among the bacteria isolated most frequently from bloodstream infections acquired in European intensive care units.[10] *Enterococcus faecium* and *Enterococcus faecalis* are the species isolated most frequently from clinical infections. In the past two decades, the prevalence of *E. faecium* has increased worldwide, mainly due to its greater ability to resist the action of antibiotics compared with *E. faecalis*.[11, 12] The incidence of *E. faecium* infections in clinical settings has risen since the 1980s along with ampicillin resistance.[12, 13] Most hospital-adapted ampicillin-resistant *E. faecium* strains belong to sequence type (ST)17, ST18, and ST78, which are part of clonal complex 17 (CC17).[14, 15] More recently, enterococci have been subdivided in two main phylogenetic groups, clade A and clade B: clade A encompasses clinical and animal isolates, whereas clade B mostly includes commensal isolates.[16, 17] Clade A enterococci are hospital-associated and encompass CC17 isolates, most of which are resistant to ampicillin and aminoglycosides and are either resistant or susceptible to vancomycin. In contrast, clade B enterococci are community-associated and are characterised by a wide antibiotic susceptibility.[18, 16]

E. faecium is intrinsically resistant to low levels of ampicillin through overproduction of the constitutive low-affinity PBP5.[19, 7] This enzyme belongs to class B PBPs (monofunctional enzymes, like PBP2B and PBP2a) and is responsible for peptidoglycan synthesis[20] when all the other PBPs are inactivated.[21, 7] The PBP5-encoding gene exists in two allelic forms, whose nucleotide sequences differ by about 5%:[22] *pbp5*-R confers an ampicillin MIC that is usually ≥ 16 mg/L and is harboured by clade A strains, whereas *pbp5*-S confers an ampicillin MIC usually ≤ 2 mg/L and is carried by clade B strains.[16, 23]

The horizontal transfer of the *pbp5* gene, including the possibility of its transfer *via* a plasmid, has been described in several papers.[24, 25, 18, 26] A recent study has documented in *E. faecium* isolates from different clonal lineages 75 PBP5 variants and the horizontal gene transfer of large chromosomal genetic platforms containing *pbp5* alleles and a number of genes involved in survival in the gastrointestinal tract.[27] However, no *pbp5*-carrying plasmids have yet been described, except in an *Enterococcus hirae* strain*;* although this plasmid has not been analysed in detail, it has been hypothesised to have been transferred from an *E. faecium* strain.[28]

In a previous study, faecal samples from healthy volunteers eating different diets were screened for AR genes.[29] A collection of intestinal lactic bacteria resistant to erythromycin and tetracycline were thus obtained and analysed. The unusual recovery of an MDR clade B commensal *E. faecium* isolate (strain 37BA) prompted this study, whose goals were to characterise the transferable plasmid pEf37BA found in *E. faecium* 37BA and to evaluate the transferability of AR traits to different bacterial genera including *Listeria*.

Materials and methods

Bacterial strain. Strain *E. faecium* 37BA was isolated in the framework of a study of the occurrence of AR genes in faecal samples from healthy volunteers eating different diets: omnivorous, ovo-lacto vegetarian, and vegan.[29] The strain was resistant to erythromycin (MIC, > 128 mg/L), ampicillin (MIC, 16 mg/L), tetracycline (MIC, 128 mg/L), streptomycin (MIC, > 128 mg/L), kanamycin (MIC, > 128 mg/L), and gentamicin (MIC, 128 mg/L) and susceptible to vancomycin (MIC, 1 mg/L) and levofloxacin (MIC, 1 mg/L). It carried the resistance genes *erm*(B), *tet*(M), *tet*(L), and *aadE*. *E. faecium* 37BA was used as the donor and *E. faecium* 64/3[30] and *Listeria welshimeri* 11857RF,[31] which are resistant to rifampicin and fusidic acid (MIC, > 128 mg/L) and susceptible to erythromycin (MIC, 0.25 mg/L) and ampicillin (MIC, 1 mg/L and 0.06 mg/L, respectively), were used as recipients in mating experiments. *L. welshimeri* was used as an alternative species to the main pathogen of the genus, *L. monocytogenes*, to assess the transferability of pEF37BA to *Listeria spp*.

Susceptibility tests. The MICs of different antibiotics – ampicillin, erythromycin, tetracycline, streptomycin, kanamycin and tigecycline (all purchased from Sigma Chemical Co., St Louis, MO, USA) – were obtained by broth microdilution and interpreted according to EUCAST and CLSI clinical breakpoints (version 8.1, www.eucast.org; CLSI 2017 M100-S27). *E. faecalis* ATCC29212 and *Staphylococcus aureus* ATCC29213 were used for quality control in susceptibility tests.

Mating experiments. Conjugal transfer was performed by filter mating as described previously.[32] Transconjugants were selected on brain heart infusion agar (BHIA; Oxoid, Basingstoke, UK) plates containing fusidic acid, rifampicin, and erythromycin (all at 10 mg/L). The transfer frequency was expressed as number of transconjugants per recipient.

SmaI- and S1-PFGE, Southern blotting, and hybridisation assays. SmaI and S1 nuclease digestion followed by PFGE analysis were performed as described previously.[33], [34] After S1-PFGE, total DNA was blotted onto positively charged nylon membranes (Ambion-Celbio, Milano, Italy) and hybridised with biotin-labelled *erm*(B) and *pbp5* probes as described elsewhere.[35]

NGS and sequence analysis. Plasmid DNA was extracted using a commercial kit (Sigma-Aldrich, St. Louis, MO, USA). NGS was carried out using Illumina HiSeq (5 Mio read pairs, 2x125 bp) technology (GenProbio srl, Parma, Italy). Contig assembly was performed with SPAdes v 3.11.1 (**http://cab.spbu.ru/software/spades/**), ORFs were annotated with RAST Annotation server (**http://rast.nmpdr.org**) and ORF Finder (**https://www.ncbi.nlm.nih.gov/orffinder**). The quality of the final contigs was improved with Burrows-Wheeler Aligner and the SAMtools suite.[36] The gaps between the plasmid contigs were closed by PCR mapping (Table S2) using primers targeting unique DNA regions and Sanger sequencing of the resulting amplicons, after purification with GenElute PCR Cleanup kit (Sigma–Aldrich). The nucleotide sequences were compared to sequences in the GenBank database using BLASTN (**http://blast.ncbi.nlm.nih.gov/blast**). The ST was determined as previously described.[33]

Amplification experiments. Primer pairs and amplicons size are reported in table S2 along with the relevant references. The Ex *Taq* system (TaKaRa Bio, Shiga, Japan) was used in amplification experiments expected to yield PCR products exceeding 3 kb in size. Excision of the *pbp5* genetic context was detected using the outward-directed pair PBP5inv-1 and PBP5inv-2 and the pair PBP5-1 and PBP5-2, which target the flanking regions of the insertion site of the *pbp5* element. The presence of the *pbp5* plasmid ($pbp5_p$) and chromosomal ($pbp5_c$) gene was sought using two specific primer pairs, **(i)** PBP5_p-FW / DWPBP5_p-RV and **(ii)** PBP5_c-FW / DWPBP5_c-RV, respectively (Table S2).

RNA extraction and reverse transcription. Each strain was grown exponentially in triplicate in brain-heart (BH) broth and diluted to $\text{OD}_{650} = 0.1$. Total RNA was extracted from 500 µl of the diluted cultures using RNeasy Mini kit (Qiagen GmbH, Hilden, Germany) according to the manufacturer's instructions. RNA purity and amount were checked with an ND-1000 Nanodrop spectrophotometer (Thermo Scientific, Wilmington, NC, USA). RNA was reverse-transcribed using QuantiTect Rev. Transcription kit (Qiagen) according to the manufacturer's recommendations.

RT-qPCR assays. Each reaction was performed in technical triplicate in a total volume of 20 µl containing 0.2 µM of each primer, 10 µl of 2 × Rotor-Gene SYBR Green PCR master mix (Qiagen), and 2 µl cDNA. RNase-free water was used as the negative control. Cycling conditions were 95°C for 5 min, followed by 35 cycles of 94°C for 10 s, 30 s of annealing, and 72°C for 20 s. A melting curve was obtained by ramping the temperature from 59°C to 95°C (0.5°C/10 s) and analysed with Qiagen's Rotor-Gene Q MDx software. Extracted RNA was tested for the absence of genomic DNA.

A delay of 12 cycles between the cDNA and the RNA quantification cycle (Cq) was considered as lack of interference. The reference genes *adk* (*E. faecium*) and *scrA* (*L. welshimeri*) were the internal controls. Qiagen's Rotor-Gene Q MDx software was employed for comparative quantification analysis of the expression level of *pbp5* in the donor, the recipient *E. faecium* 64/3 and the two transconjugants using *E. faecium* 37BA as the calibrator.[37] The results are reported as the average of three biological replicates in three RT-qPCR assays ± standard deviation.

Stability of pEf37BA. The stability of the *pbp5*-carrying plasmid was evaluated by serial daily passages on antibiotic-free BHIA. Every week some colonies were tested by MIC determination for ampicillin susceptibility and by PCR mapping to detect the pEf37BA plasmid.

Nucleotide sequence accession number. The nucleotide sequence of pEF37BA plasmid has been deposited in GenBank under accession number MG957432.

Results

Conjugation experiments and PCR assays. To confirm the transferability of *erm*(B) and evaluate its possible association with mobile genetic elements, *E. faecium* 37BA was used as a donor in filter mating experiments. *erm*(B) was successfully transferred to *E. faecium* 64/3 and *L. welshimeri* 11857RF at a frequency of 5.7×10^{-4} and 8.5×10^{-8} per recipient cell, respectively. Two transconjugants, *E. faecium* 6B2 and *L. welshimeri* TW2, were selected for further investigation. Their match with the recipient was confirmed by comparing their SmaI-PFGE profiles with those of the donor and the recipient (Figure S1). The erythromycin MIC and PCR amplification assays indicated that both were fully resistant to erythromycin (MIC, > 128 mg/L) and carried *erm*(B) (Table 1). Moreover, both transconjugants also acquired *tet*(M), *tet*(L), and *aadE* from the donor (Table 1).

Plasmid location of the *erm*(B) gene. The location of the *erm*(B) gene in the donor *E. faecium* 37BA and in the two transconjugants *E. faecium* 6B2 and *L. welshimeri* TW2 was investigated by S1–PFGE followed by Southern blotting. S1-PFGE revealed that the donor and *E. faecium* 6B2 both harboured two plasmids of ~40 and ~200 kb, whereas *L. welshimeri* TW2 carried a single plasmid of ~ 40 kb. Hybridisation assays showed that *erm*(B) was located on the ~40 kb plasmid in all strains (Figure 1).

NGS analysis and characterisation of a new mosaic MDR plasmid carrying the *pbp5* gene. NGS analysis of the donor *E. faecium* 37BA and the two transconjugants, *E. faecium* 6B2 and *L. welshimeri* TW2, showed that the complete sequence of the *erm*(B)-carrying plasmid, pEf37BA, had a size of 40,396 bp and a G+C content of 36.0% (accession no. MG957432). Sequence analysis identified 44 ORFs encoding proteins ≥ 50 amino acids. The genetic map of pEf37BA is shown in figure 2, along with the maps of elements showing high nucleotide similarity and the main ORF features. BLAST analysis revealed a high nucleotide identity with four different AR elements in the following four pEf37BA regions:

(i) Region of erythromycin resistance (*1 – 1,351 bp; G+C content, 33%*). This *erm*(B) (*orf1*)-carrying region showed 99% nucleotide identity with the *erm*(B)-containing segments found in some enterococcal plasmids [*E. faecium* DO plasmid 2 (accession no. NC_017962.1); *E. faecalis* V583 plasmid pTEF1 (accession no. NC_004669.1)].

(ii) Region of multidrug resistance (*1,352 – 15,595 bp; G+C content, 36%*). This region carried six AR genes – *aadE* (*orf2* and *orf14*), *spw* (*orf4*), *lsa*(E) (*orf8*), *lnu*(B) (*orf9*), *sat4* (*orf15*), and *aphA* (*orf16*) – which confer resistance to streptomycin, spectinomycin, lincosamide-streptogramin-pleuromutilin, lincosamide, streptothricin, and kanamycin, respectively. This region exhibited 99% nucleotide identity with a chromosomal multiresistance gene cluster of *Erysipelothrix rhusiopathiae* (accession no. MF405337.1).

(iii) Region of ampicillin resistance (*15,595 – 20,912 bp, G+C content, 38%*). This region contained the *pbp5* cluster including the *pbp5* repressor (*orf21*) and the *pbp5* structural gene (*orf22*), which are responsible for β-lactam resistance, and exhibited 100% identity with the *pbp3r* of *E. hirae* (accession no. X69092).[28] Remarkably, the *pbp5* gene sequence showed 99% nucleotide identity with the previously described *pbp5* of *E. faecium* BM4107 (C46 variant, accession no. AF364092.1).[38] Alignment of the two amino acid sequences, which showed 100% similarity and 99% identity, demonstrated two mismatches at positions S39T and D644N (Figure S2). The genetic context of *pbp5* was bounded by two identical IS*1216* transposase genes (*orf20* and *orf23*) with the same orientation, which were flanked by 23 bp (GGTTCTGTTGCAAAGTTTTAAAT) inverted repeats. The *pbp5* element was integrated within *orf19*, encoding riboflavin biosynthesis protein RibD (Table 2), leading to loss of 406 bp of the gene. This segment exhibited 99% nucleotide identity with a region of an *E. hirae* plasmid (accession no. X69092.1)[28] and several chromosomal segments of *E. faecium*. PCR and sequencing (Table S1) demonstrated the ability of this region to loop out, resulting in a circular form that contained *pbp5*, the repressor gene and an IS*1216*, and leaving a single IS*1216* copy at the excision site.

(iv) Region of tetracycline resistance (*20,103 – 40,396 bp; G+C, content 35%*). This region contained the tetracycline resistance genes *tet*(L) and *tet*(M), which were arranged in tandem (*orf41* and *orf42*), and three genes (*orf31, orf32*, and *orf33*), which are involved in plasmid replication, including a *repA* belonging to the *rep*$_2$ family.[39] This region exhibited 99% DNA identity to the 19,557 bp *E. faecium* plasmid pM7M2 (accession no. JF800907).[40]

NGS analysis also showed the presence of a ~200 kb mega plasmid (not completely assembled) carrying a complete transfer machinery in the donor *E. faecium* 37BA and in the transconjugant *E. faecium* 6B2, in a region showing 99% nucleotide identity (cover, 97%) with the pNB2354_1 plasmid (214,319 bp) of *E. faecium* NRRL B-2354 (accession no. CP004064). This region contained a pilus assembly and the *traG*, *virB4*, and topoisomerase-primase *ltrC*-like genes. *repA* gene, which was classified as rep20/pLG1, was also detected.[41] Interestingly, β-lactam resistance genes were not detected in the mega plasmid.

Susceptibility assays and MLST. Carriage by pEf37BA of *pbp5* and additional AR genes prompted the analysis of the antibiotic susceptibility patterns of *E. faecium* 37BA, *E. faecium* 6B2, and *L. welshimeri* TW2. All strains were resistant to erythromycin, tetracycline, streptomycin, and kanamycin and fully susceptible to tigecycline; *E. faecium* 37BA and *E. faecium* 6B2 were also resistant to ampicillin (Table 1).

The MLST data showed that *E. faecium* 37BA belonged to ST253 (clade B, which encompasses commensal strains).[42]

***pbp5* gene expression and location.** To explain the ampicillin susceptibility of the transconjugant *L. welshimeri* TW2, *pbp5* expression was assayed by RT-qPCR in the donor *E. faecium* 37BA, in the recipient *E. faecium* 64/3 and in the two transconjugants *E. faecium* 6B2 and *L. welshimeri* TW2, all of which carried pEf37BA, except for the recipient. Genomic DNA interference was detected in none of the RNA extracts, since the Cq delay between cDNA and RNA was over the fixed cut-off (12 cycles) and the reference genes were correctly amplified. Interestingly, the donor and the transconjugants exhibited comparable *pbp5* transcription levels, and the recipient strain *E. faecium* 64/3 showed a 10-fold lower expression of the same gene (Figure 3).

PCR assays indicated that both the donor, *E. faecium* 37BA, and transconjugant *E. faecium* 6B2 harboured two copies of the *pbp5*, one plasmid ($pbp5_p$) and one chromosomal ($pbp5_c$) located. This results was confirmed by S1-PFGE, followed by hybridisation with a *pbp5* probe (data not shown), and sequencing.

pEf37BA stability assays. *E. faecium* 37BA, *E. faecium* 6B2, and *L. welshimeri* TW2 were maintained for 30 days in antibiotic-free BHIA. A modification in the ampicillin MIC and the loss of pEf37BA were never recorded.

Discussion

In enterococci, conjugative plasmids are the main elements involved in the horizontal transfer of AR genes.[43], [44] Recombination through IS elements allows the exchange of DNA segments between chromosomes and plasmids, enhancing the spread of AR traits.[45], [18]

The unusual recovery of a commensal *E. faecium* isolate showing multidrug resistance (strain 37BA) prompted its extensive characterisation and the investigation of its ability to transfer AR genes. The strain was first used as the donor in intra- and interspecific conjugation assays involving selection for erythromycin resistance. The donor and the two transconjugants selected for analysis, *E. faecium* 6B2 and *L. welshimeri* TW2, harboured a ~40 kb *erm*(B)-carrying plasmid. Sequencing revealed a new MDR plasmid (which we named pEf37BA) that resulted from the recombination of the *E. faecium* plasmid pM7M2 and an MDR chromosomal region of *E. rhusiopathiae*. *E. rhusiopathiae* causes the disease known as erysipelas, which may affect a wide range of animals. Although it is primarily considered as an animal pathogen, the bacterium can also cause erysipeloid, a zoonotic infection affecting humans. Since the genera *Erysipelotrix* and *Enterococcus* belong to different classes, the presence of an *E. rhusiopathie* DNA region in an *E. faecium* plasmid highlights the ability of the former bacterium to transfer DNA to distantly related bacteria, possibly through IS-mediated recombination. This mechanism thus seems responsible for the construction of the mosaic plasmid pEf37BA, which is characterised by a high potential of AR gene dissemination.

Besides *erm*(B), pEf37BA also harboured a large number of AR determinants, including a region coding for PBP5. Differently from earlier work,[27] this region was integrated in an *orf* (*orf 19*) encoding a riboflavin biosynthesis protein and showed high-level identity with several enterococcal chromosomal regions and with a portion of a not completely characterised *E. hirae* plasmid.[28] Although the transferable nature of the *pbp5* determinants in *E. faecium* has been described in several studies,[18, 24-26] to the best of our knowledge this is the first report of a *pbp5* element carried by a transferable MDR plasmid of *E. faecium*. This genetic context showed high identity with the chromosomal *pbp5* of *E. faecium* and was inserted in a region flanked by two IS*1216* having the same orientation and capable of looping out from the plasmid by IS*1216*-mediated transposition. These findings suggest the IS*1216*-mediated transposition of a *pbp5*-carrying region from the *E. faecium* chromosome to the plasmid pEf37BA.

To date, 75 PBP5 protein variants have been described in ampicillin-resistant and -susceptible strains. The one detected in our clade B commensal strain was an additional variant differing from the C46 variant of *E. faecium* BM4107, which is commonly found in clade A hospital-adapted isolates, by only two mutations, S39T and D644N.[27]

The transcription level of the *pbp5* gene was comparable in the donor and in the two transconjugant, and was 10 times lower in *E. faecium* 64/3, which only harboured the *pbp5* chromosomal copy. Despite this, the *L. welshimeri* transconjugant was fully susceptible to ampicillin, with an MIC identical to that of the recipient. This behaviour may be ascribed to post-transcriptional regulation or to incorrect protein folding resulting in lack of activity. Moreover, in *E. faecium* β-lactam resistance can depend on the expression of additional genes. Wall biosynthesis is ensured by co-operation of transpeptidase PBP5 with high molecular-weight bifunctional class A PBPs, *i.e.* PBPs exhibiting both transglycosylase and transpeptidase activity.[27, 20] Therefore, it cannot be excluded that the resistance phenotype detected in the *E. faecium* strains is due to interactions with species-specific PBPs that are not found in *L. welshimeri*.

The tetracycline resistance region of pEf37BA corresponded to the complete pM7M2 of the dairy strain *E. faecium* M7M2,[40] which contains the tetracycline resistance genes *tet*(M) and *tet*(L) arranged in tandem. The association of the two genes has been described in three tetracycline-resistant *E. faecium* plasmids, pDO1[46], pLAG[36] and a tet(L)/tet(M)$_p$ plasmid, the latter conferring high-level resistance to tigecycline in clinical enterococci.[47]

Transferable plasmids can be mobilised by a co-resident conjugative element both in *trans* and in *cis*.[43] We have recently described the ability of a pHTβ-like plasmid to mobilise two co-resident non-conjugative MDR plasmids, pRUM$_{17i48}$ and the newly described pLAG, which lack a transfer machinery.[36] The present findings show that pEf37BA can spread not only to other enterococci, but also to different genera such as *Listeria*. Plasmidome analysis demonstrated that the donor *E. faecium* 37BA and the transconjugant *E. faecium* 6B2 harboured two plasmids (~ 40 – 200 kb), whereas the transconjugant *L. welshimeri* TW2 harboured a single ~40 kb plasmid. Interestingly, sequence analysis demonstrated a ~ 200 kb mega plasmid lacking β-lactam resistance genes and containing a complete transfer machinery. Since we found no complete conjugation region in pEf37BA and no cointegrate, either in the donor or in *E. faecium* 6B2, it may be hypothesised that pEf37BA underwent *trans*-mobilisation *via* the transfer apparatus encoded by the co-resident mega plasmid. The presence of a single ~40 kb plasmid in *L. welshimeri* TW2 can be explained by the transfer of pEf37BA to the transconjugant through the conjugation machinery encoded by the mega plasmid, which may be unable to replicate in *Listeria*.

The conjugal transfer of AR genes in enterococci is a well-known phenomenon.[43] Indirect evidence of *pbp5* transfer between *E. faecium* strains *via* plasmid intermediaries has been provided by García-Solache and colleagues, who however did not identify the genetic element responsible for the transfer.[26] The present data provide the first evidence of the ability of the *pbp5* gene to undergo plasmid-mediated transfer and of the ability of a *pbp5*-carrying plasmid to be transferred and to replicate in different genera such as *Listeria.* Transfer from the non-pathogenic *L. welshimeri* to the main food-borne pathogen *L. monocytogenes* seems likely, as suggested by Katharios-Lanwermeyer and co-workers.[48] Although the *pbp5* gene did not confer a resistance phenotype on *L. welshimeri*, the pEf37BA plasmid may contribute to spread the *pbp5* gene among different species, also considering its persistence in the absence of selective pressure

Altogether, these findings have the potential to advance our understanding of the dissemination of ampicillin resistance among *E. faecium* strains. They show that *pbp5* horizontal gene transfer can be associated not only with the movement of large chromosomal DNA regions,[26, 27] but also with plasmid transfer. The identification of a *pbp5*-carrying MDR plasmid in a commensal *E. faecium* strain is a cause for concern, since it further documents the spread of antibiotic, including ampicillin resistance in the commensal clade B E. *faecium* lineage, which can contribute to the spread of ampicillin resistance to the major hospital-adapted *E. faecium* clones and to different bacterial genera that can be found in the gut microhabitat, including the food-borne pathogen *L. monocytogenes*.

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Transparency declarations

None to declare.

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Figure legends

Figure 1. S1-PFGE plasmid profiles of donor, transconjugants, and recipients **(A)** and hybridisation with the *erm*(B) probe **(B)**. M, DNA molecular weight low-range PFG marker (New England Biolabs, Ipswich, MA, USA). The size (kb) of fragments is reported on the left; lane 1, *E. faecium* 37BA; lane 2, *E. faecium* 6B2; lane 3, *E. faecium* 64/3; lane 4, *L. welshimeri* TW2; line 5, *L. welshimeri* 11857RF.

Figure 2. Genetic organisation of the *E. faecium* pEf37BA (accession no. MG957432), the *E. faecium* pM7M2 (accession no. JF800907), the *E. rhusiopathiae* multiresistance ZJ region (accession no. MF405337.1) and the *E. hirae pbp3r* (accession no. X69092.1) cluster. Similar ORFs, of different genetic elements, are represented by black arrows pointing in the direction of transcription. Antibiotic resistance genes are in red and IS*1216* in grey. The light grey areas between ORFs denote DNA identities ≥ 99%.

Figure 3. *pbp5* gene expression analysis in the donor *E. faecium* 37BA, recipient *E. faecium* 64/3, and transconjugants *E. faecium* 6B2 and *L. welshimeri* TW2. *E. faecium* 37BA was considered as the calibrator (100%). The results are reported as the average of three biological replicates in three RT-qPCR assays ± standard deviation.

FIGURE 1

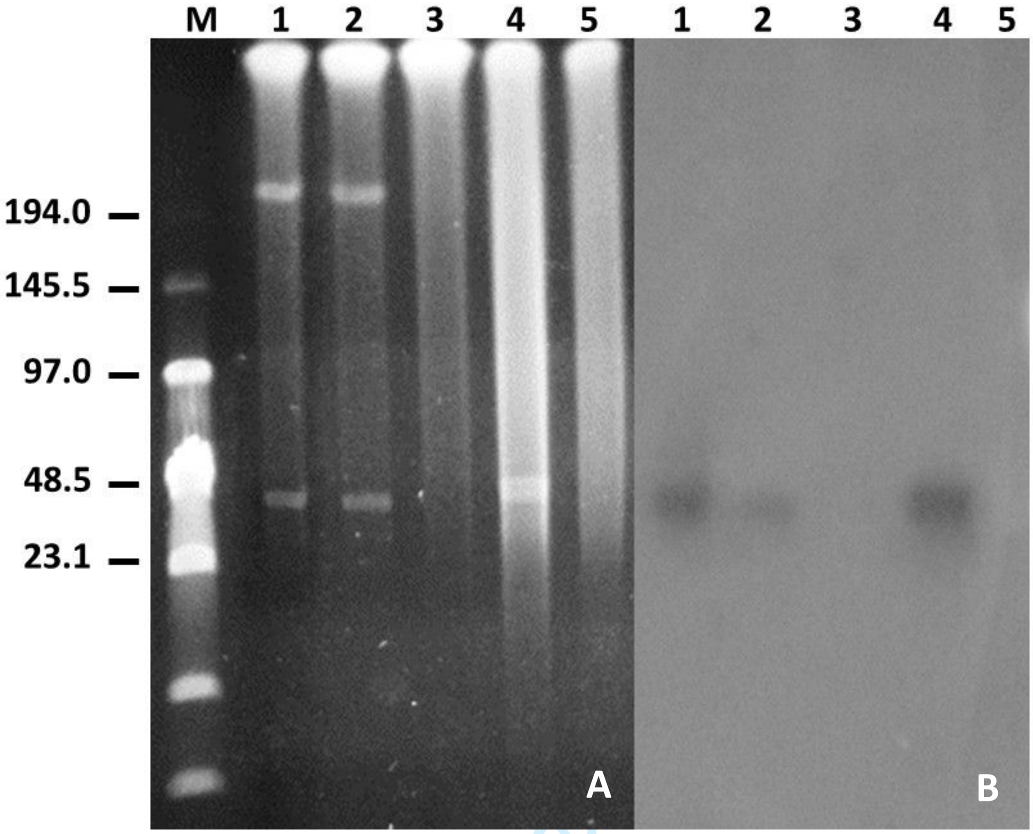
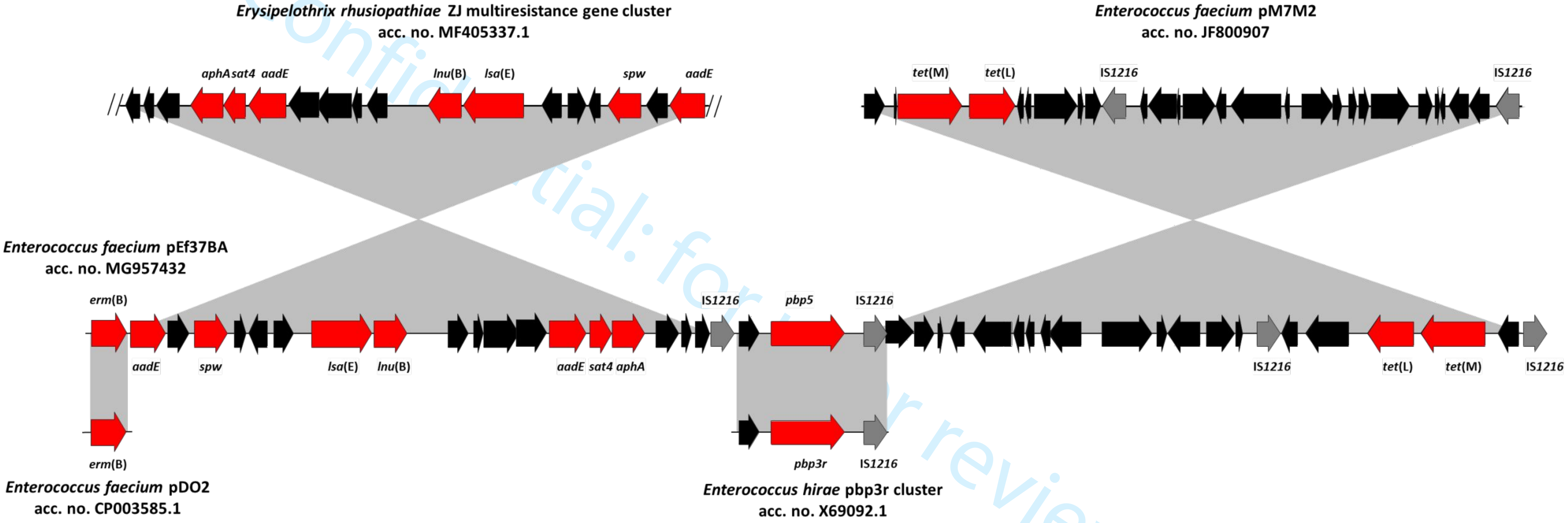


FIGURE 2


Erysipelothrix rhusiopathiae ZJ multiresistance gene cluster
acc. no. MF405337.1
aphA sat4 aadE
lnu(B) lsa(E)
spw
aadE
Enterococcus faecium pM7M2
acc. no. JF800907
tet(M)
tet(L)
IS1216
IS1216
Enterococcus faecium pEf37BA
acc. no. MG957432
erm(B)
aadE
spw
lsa(E)
lnu(B)
aadE sat4 aphA
IS1216
pbp5
IS1216
IS1216
tet(L)
tet(M)
IS1216
erm(B)
Enterococcus faecium pDO2
acc. no. CP003585.1
pbp3r
IS1216
Enterococcus hirae pbp3r cluster
acc. no. X69092.1

513 **FIGURE 3**

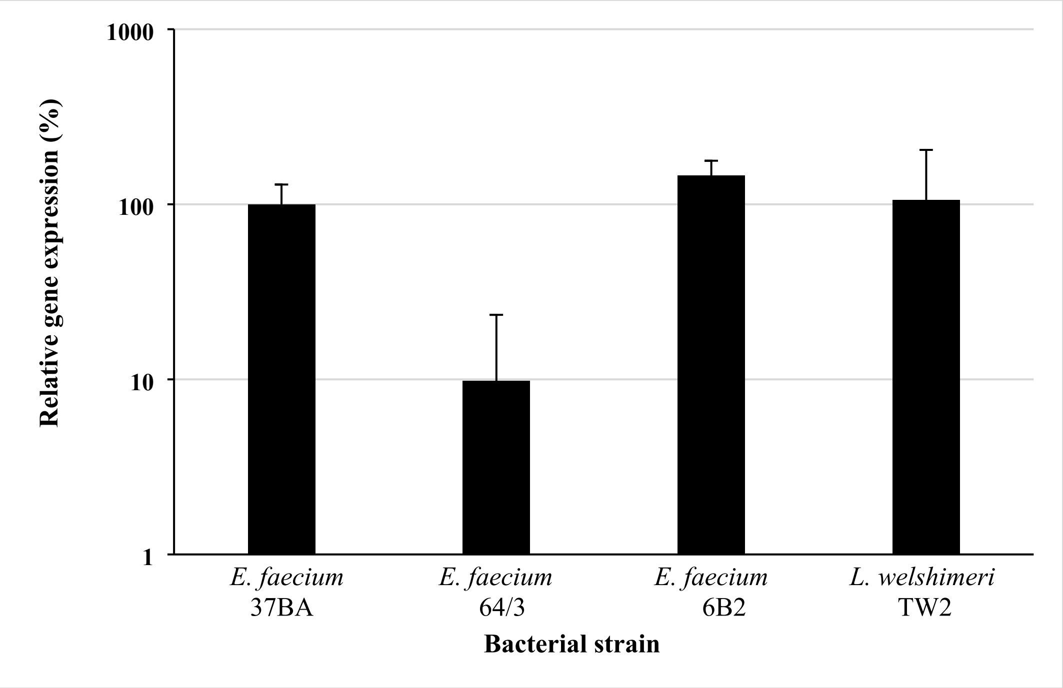

1000
100
10
1
Relative gene expression (%)
E. faecium 37BA
E. faecium 64/3
E. faecium 6B2
L. welshimeri TW2
Bacterial strain

Table 1. Conjugal transfer of pEf37BA from the donor *E. faecium* 37BA to recipients *E. faecium* 64/3 and *L. welshimeri* 11857RF.

Strain	Genotype	Transfer Frequency	MIC (mg/L)[a]					
			ERY	TET	STR	KAN	AMP	TIG
E. faecium 37BA (D)	*tet*(M), *tet*(L), *sat4* *aadE*, *aphA*, *spw*, *erm*(B) *lsa*(E), *lnu*(B), *pbp5*$_{p}$[b], *pbp5*$_{c}$[c]		>128	16	>128	>128	16	0.25
E. faecium 6B2 (T)	*tet*(M), *tet*(L), *sat4* *aadE*, *aphA*, *spw*, *erm*(B) *lsa*(E), *lnu*(B), *pbp5*$_{p}$, *pbp5*$_{c}$	5.7 x 10^{-4}	>128	16	>128	>128	16	0.125
E. faecium 64/3 (R)	*pbp5*$_{c}$		0.25	1	2	32	1	0.125
L. welshimeri TW2 (T)	*tet*(M), *tet*(L), *sat4* *aadE*, *aphA*, *spw*, *erm*(B) *lsa*(E), *lnu*(B), *pbp5*$_{p}$	8.5 x 10^{-8}	>128	4	>128	128	0.125	0.015
L. welshimeri 11857RF (R)			0.125	0.5	8	2	0.06	0.015

Abbreviations: (D) donor, (T) transconjugant, (R) recipient.

[a] ERY, erythromycin; TET, tetracycline; STR, streptomycin; KAN, kanamycin; AMP, ampicillin; TIG, tigecycline.

[b] *pbp5*$_{p}$, plasmid *pbp5*

[c] *pbp5*$_{c}$, chromosomal *pbp5*.

Supplementary data

Table S1. Amino acid sequence identities/similarities of putative proteins encoded by the plasmid pEf37BA (GenBank accession no. MG957432).

ORF	Start (bp)	Stop (bp)	Size (amino acids)	Predicted function	BLASTP analysis[a] Most significant database match	Accession no.	% Amino acid identity
orf1	336	1,073	245	Ribosomal RNA adenine dimethylase	Erm(B) [*Streptococcus agalactiae*]	WP_079275877.1	100
orf2	1,378	2,241	287	Aminoglycoside 6- adenylyltransferase	Streptomycin adenylyltransferase [*Streptococcus suis* BM407]	YP_003028700.1	100
orf3	2,285	2,812	175	Adenine/guanine phosphoribosyltransferase	Adenine phosphoribosyltransferase [Bacteria]	WP_002294507.1	100
orf4	3,025	3,753	242	Aminoglycoside resistance protein	Aminoglycoside nucleotidyltransferase Spw [Bacteria]	WP_002294509.1	100
orf5	3,971	4,222	83		Hypothetical protein [Firmicutes]	WP_002294510.1	100
orf6	4,731	4,273	152		Hypothetical protein [Firmicutes]	WP_002325145.1	100
orf7	4,793	5,377	194	Recombinase zinc β ribbon domain	DNA recombinase [Firmicutes]	WP_088186203.1	99
orf8	5,820	7,304	494	ATPase components of ABC transporters	ABC-F type ribosomal protection protein Lsa(E) [Firmicutes]	WP_002294513.1	100
orf9	7,358	8,157	267		Lincosamide nucleotidyltransferase Lnu(B) [Firmicutes]	WP_002294514.1	100
orf10	9,002	9,670	137	Recombinase zinc β ribbon domain	Recombinase [Firmicutes]	WP_002303394.1	99
orf11	9,813	10,037	74	Transcriptional regulator	XRE family transcriptional regulator [Firmicutes]	WP_002303393.1	100
orf12	10.052	10,921	289	Nucleotidyltransferase domain	Hypothetical protein [Bacilli]	WP_002303392.1	100
orf13	10,902	11,636	244	Methyltransferase domain	Hypothetical protein pRUM_p17 (plasmid) [*E. faecium*]	NP_863160.1	100
orf14	11,669	12,577	302	Streptomycin adenylyltransferase	Streptomycin aminoglycoside 6-adenyltransferase (plasmid) [*E. faecium*]	NP_863159.1	100
orf15	12,586	13,116	176	Acetyltransferase (GNAT) family	Streptothricin acetyltransferase (plasmid) [*E. faecium*]	79 (89)	100
orf16	13,209	14,003	264	Aminoglycoside 3'-phosphotransferase	Aminoglycoside phosphotransferase type III (plasmid) *[Enterococcus faecalis]*	YP_783930.1	100
orf17	14,486	14,851	121	DNA-binding transcriptional regulator	ESAT-6 gene cluster (plasmid) [*Staphylococcus aureus*]	YP_006937248.1	100
orf18	14,956	15,231	91		Hypothetical protein [*S. aureus*]	WP_016169115.1	100
Δorf19	15,306	15,632	108	Pyrimidine reductase, riboflavin biosynthesis	Riboflavin biosynthesis protein RibD [*Streptococcus suis*]	WP_042507186.1	98
orf20	15,664	16,350	228	Transposase	IS*6*-like element IS*1216* family transposase [*E. faecium*]	WP_014748744.1	100
orf21	16,491	17,375	294	Anionic cell wall polymer biosynthesis enzyme LytR-Cps2A-Psr (LCP) family	LytR family transcriptional regulator [*Enterococcus*]	WP_002309184.1	100
orf22	17,506	19,542	678	NTF2-like N-terminal transpeptidase domain	Penicillin-binding protein 4 [*Enterococcus*]	WP_002348439.1	100
orf23	20,171	20,857	228	Transposase	IS*6*-like element IS*1216* family transposase [*E. faecium*]	WP_014748744.1	100

orf24	21,055	21,660	201	Fic/DOC family protein	Putative cell filamentation protein (plasmid) [*E. faecalis*]	YP_783935.1	100
orf25	21,676	22,248	190	Serine Recombinase	Putative resolvase (plasmid) [*E. faecalis*]	YP_783936.1	100
orf26	22,362	22,520	52		Hypothetical protein pEF1_p17 (plasmid) [*E. faecium*]	YP_001966117.1	100
orf27	23,143	22,721	140	Transposase	Transposase (plasmid) [*E. faecium*]	YP_004849412.1	100
orf28	24,230	23,394	278	Transposase	Putative transposase (plasmid) [*E. faecalis*]	YP_783937.1	100
orf29	24,556	24,266	96	Transposase	Hypothetical protein pRE25p57 (plasmid) [*E. faecalis*]	YP_783939.1	100
orf30	25,216	24,962	84	Transposase	IS3/IS911 family transposase (plasmid) [*E. faecium* DO]	YP_006377323.1	100
orf31	25,684	25,409	91		Putative PrgO protein (plasmid) [*E. faecalis*]	YP_783940.1	100
orf32	26,609	25,656	317	Protein implicated in chromosome segregation	Putative PrgP protein (plasmid) [*E. faecalis*]	YP_783941.1	100
orf33	27,221	28,714	497	Primase	Putative Rep protein (plasmid) [*E. faecalis*]	YP_783885.1	100
orf34	28,828	29,145	105		PrgN (plasmid) [*E. faecium*]	YP_001966129.1	100
orf35	30,128	29,169		Transposase	Integrase (plasmid) [*E. faecium*]	YP_004849403.1	100
orf36	30,311	31,162			Hypothetical protein pVEF1_028 (plasmid) [*E. faecium*]	YP_976091.1	100
orf37	31,165	31,395	76		Hypothetical protein -pVEF3_p39 (plasmid) [*E. faecium*]	YP_001974809.1	100
orf38	31,810	32,508	232	Transposase	IS*6*-like element IS*1216* family transposase [*E. faecium*]	WP_014748744.1	100
orf39	33,036	32,542	164	Plasmid rolling circle replication initiator protein REP	Protein rep [*Enterococcus*]	WP_025481467.1	100
orf40	34,522	33,260	420	Plasmid recombination enzyme	Mob (plasmid) [*Bacillus cereus*]	NP_043522.1	100
orf41	36,462	35,086	459	Major Facilitator Superfamily	Tetracycline resistance protein (plasmid) [*Streptococcus agalactiae*]	NP_040422.1	99
orf42	38,575	36,656	639	Tetracycline resistant protein	Tetracycline resistance protein TetM (plasmid) [*E. faecium*]	YP_004849392.1	100
orf43	39,569	38,952	205	Conjugative transposon protein	Conjugal transfer protein [*Enterococcus*]	WP_014088861.1	100
orf44	39,710	40,396	228	Transposase	IS*6*-like element IS*1216* family transposase [*E. faecium*]	WP_014748744.1	100

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[a] For each ORF, only the most significant identity detected is listed.
[b] Δ represented a truncated ORF.

Table S2 Primer pairs, target genes, and amplicon size

Gene	Primer Designation	Sequence (5'-3')	Reference	Product size (bp)
Resistance genes				
erm(B)[a]	ERMB1	GAAAAGGTACTCAACCAAATA	1	638
	ERMB2	AGTAACGGTACTTAAATTGTTTAC		
tet(M)	TETM2	GAACTCGAACAAGAGGAAAGC	2	740
	TETM3	ATGGAAGCCCAGAAAGGAT		
tet(L)	TETL1	ATAAATTGTTTCGGGTCGGTAAT	3	1,077
	TETL2	AACCAGCCAACTAATGACAATGAT		
aadE	AADE1	CAAGGGAGTATGATGATTGCTGC	This study	250
	AADE2	TAGTTCTGCTACCTCTTTGGACAC		
pbp5[a]	PBP5-1	ATCCAAACAAAATGACAAACGG	This study	292
	PBP5-2	TGCCAATGGAATCCCTAAAGCAGAAA		
pbp5$_c$[b]	PBP5$_c$-FW	ATCTTAATAGCAGCTGCGG	This study	2,323
	DWPBP5$_c$-RV[c]	CAGAATAAGAAAAATGACTA		
pbp5$_p$[d]	PBP5$_p$-FW	ATTTTAATAGTAACTGCAA	This study	2,300
	DWPBP5$_p$-RV[e]	TCTGACCCCCGATAGATTTTT		
Assessment of the stability of the pbp5 genetic context				
pbp5	PBP5inv-1	CCGTTTGTCATTTTGTTTGGAT	This study	
	PBP5inv-2	TTTCTGCTTTAGGGATTCCATTGGCA		
orf19	PBP5-up	CAAGCCCGGAGGACCCCAGACC	This study	
*orf24*up	PBP5-down	TCTGACCCCCGATAGATTTTT		
RT-qPCR assays				
pbp5	PBP5F	TGTAAATGGTACAGCACATTC	4	127
	PBP5R	GTTGAAAGCAAACAAGAAACT		
adk	adkF	GCTTCTTATTAGATGGCTTTCC	4	125
	adkR	GACCAAGATTTCTTCACCAACA		
scrA	scrALWelF	CTCCCACATTGGTGCTACTC	5	94
	scrALWelR	GATTCCGTTCACTAATCCATCAG		
PCR mapping of the pEF37BA plasmid				
erm(B)	ERMB1	GAAAAGGTACTCAACCAAATA	1	11,980
aadE	AADE2	CGGTAGGTGGACAAAAGTT	This study	
aadE	AADE1	CAAGGGAGTATGATGATTGCTGC	This study	8,854
orf23-dw	NODO3FW	TCTGACCCCCGATAGATTTTT		
orf23-up	NODO4FW	TACTTCTTCTTTGACCTTTGT	This study	16,185
tet(L)	TETL1	ATAAATTGTTTCGGGTCGGTAAT	3	
tet(L)	TETL2	AACCAGCCAACTAATGACAATGAT	3	6,289
erm(B)	ERMB2	AGTAACGGTACTTAAATTGTTTAC	2	

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[a] The primer pairs ERMB1/ERMB2 and PBP5-1/PBP5-2 were used to obtain a specific probe.

[b] *pbp5*$_c$, chromosomal *pbp5*

[c] primer located downstream to chromosomal *pbp5*, specific for the *E. faecium* 64/3 genome (accession no. NZ_CP012522.1)

[d] *pbp5*$_p$, plasmid *pbp5*.

[e] primer located downstream to plasmid *pbp5*, specific for the pEf37BA plasmid.

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5. Hage, E., Mpamugo, O., Ohai, C. *et al*. Identification of six *Listeria* species by real-time PCR assay. Lett Appl Microbiol. 2014; **58**:535-40.

Figure S1. SmaI-PFGE patterns of the donor *E. faecium* 37BA (donor), the recipients *E. faecium* 64/3 and *L. welshimeri* 11857RF, and the two transconjugants *E. faecium* 6B2 and *L. welshimeri* TW2. Lane 1, DNA molecular weight low-range PFG marker (New England Biolabs, Ipswich, MA. USA); the size (kb) of the fragments is reported on the left; lane 2, *E. faecium* 37BA; lane 3, *E. faecium* 6B2; lane 4, *E. faecium* 64/3; lane 5, *L. welshimeri* TW2; lane 6, *L. welshimeri* 11857RF.

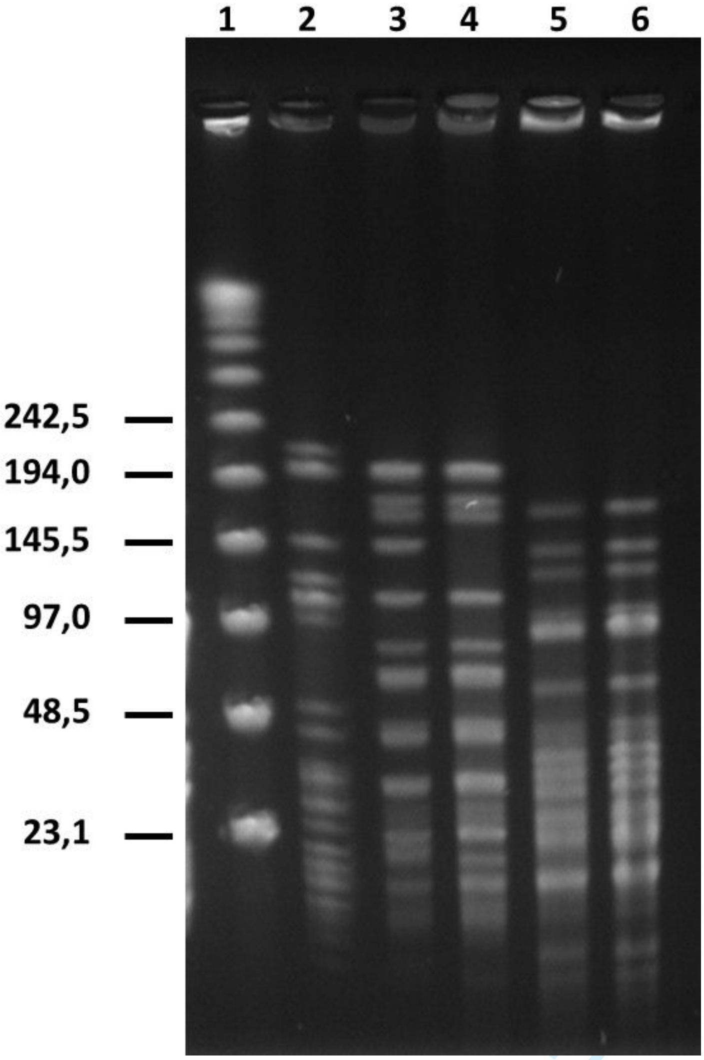

Figure S2. Amino acid sequence alignment of the *pbp5* gene of *E. faecium* BM4107 and 37BA. Mismatches are in bold type and highlighted in gray.

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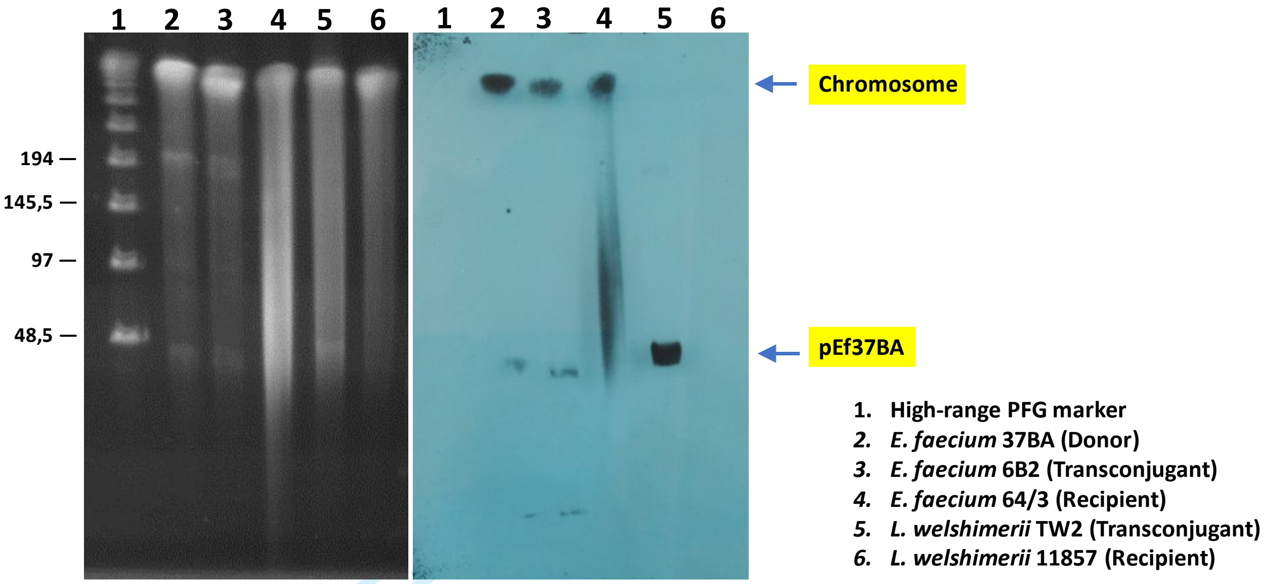

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3. *E. faecium* 6B2 (Transconjugant)
4. *E. faecium* 64/3 (Recipient)
5. *L. welshimerii* TW2 (Transconjugant)
6. *L. welshimerii* 11857 (Recipient)

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ACCESSION
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DEFINITION  Enterococcus faecium 37BA
ACCESSION
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ORGANISM    Enterococcus faecium 37BA
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LOCUS       Contig 13                 4094 bp    DNA     linear   UNK
DEFINITION  Enterococcus faecium 37BA
ACCESSION
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BASE COUNT     1381 a    727 c    745 g   1241 t

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DEFINITION  Enterococcus faecium 37BA
ACCESSION
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Below are indicated contigs of the mega plasmid not annotated by RAST

>Contig 15

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