



Antimicrobial Resistance of Salmonella enterica Serovar Typhimurium in Shanghai, China

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Wang J, Li Y, Xu X, Liang B, Wu F, Yang X, Ma Q, Yang C, Hu X, Liu H, Li H, Sheng C, Xie J, Du X, Hao R, Qiu S and Song H (2017) Antimicrobial Resistance of Salmonella enterica Serovar Typhimurium in Shanghai, China. Front. Microbiol. 8:510. doi: 10.3389/fmicb.2017.00510 ¹ Institute of Disease Control and Prevention, Academy of Military Medical Sciences, Beijing, China, ² Western Theater Command, Tianshui, China, ³ The Key laboratory of Pharmacology and Molecular Biology, Medical College, Henan University of Science and Technology, Luoyang, China, ⁴ Shanghai Municipal Center for Disease Control and Prevention, Shanghai, China

We aimed to analyze the antimicrobial resistance phenotypes and to elucidate the molecular mechanisms underlying resistance to cephalosporins, ciprofloxacin, and azithromycin in Salmonella enterica serovar Typhimurium isolates identified from patients with diarrhea in Shanghai. The isolates showed high rates of resistance to traditional antimicrobials, and 20.6, 12.7, and 5.5% of them exhibited decreased susceptibility to cephalosporins, ciprofloxacin, and azithromycin, respectively. Notably, 473 (84.6%) isolates exhibited multidrug resistance (MDR), including 161 (28.8%) isolates that showed an ACSSuT profile. Twenty-two MDR isolates concurrently exhibited decreased susceptibility to cephalosporins and ciprofloxacin, and six of them were co-resistant to azithromycin. Of all the 71 isolates with decreased susceptibility to ciprofloxacin, 65 showed at least one mutation (D87Y, D87N, or D87G) in gyrA, among which seven isolates simultaneously had mutations of parC (S80R) (n = 6) or parC (T57S/S80R) (n = 1), while 49 isolates with either zero or one mutation in gyrA contained plasmidmediated quinolone resistance (PMQR) genes including gnrB, gnrS, and aac(6')-lb-cr. Among the 115 cephalosporin-resistant isolates, the most common ESBL gene was bla_{CTX-M}, followed by bla_{TEM-1}, bla_{OXA-1}, and bla_{SHV-12}. Eight subtypes of bla_{CTX-M} were identified and $bla_{CTX-M-14}$ (n = 22) and $bla_{CTX-M-55}$ (n = 31) were found to be dominant. To the best of our knowledge, this is the first report of the presence of blaCTX-M-123 and blacTX-M-125 in S. Typhimurium. Besides, mphA gene was identified in 15 of the 31 azithromycin-resistant isolates. Among the 22 isolates with reduced susceptibility to cephalosporins and ciprofloxacin, 15 contained ESBL and PMQR genes. Coexistence of these genes lead to the emergence of MDR and the transmission of them will pose great difficulties in S. Typhimurium treatments. Therefore, surveillance for these MDR isolates should be enhanced.

Keywords: Salmonella, ESBL, ciprofloxacin, azithromycin, PMQR

INTRODUCTION

Salmonella infection is a major global public health problem, which has caused food-borne illnesses in many countries. Data from the Foodborne Diseases Active Surveillance Network (Foodnet) report showed that Salmonella has become a leading cause of death as a food-borne bacterial pathogens in the United States (Barton Behravesh et al., 2011). Among the more than 2500 serotypes of Salmonella (Popoff et al., 2001), S. Typhimurium is one of the predominant serotypes in many developed and developing countries, and the global outbreak of food-borne diseases due to infection by S. Typhimurium is impressive. S. Typhimurium infection was very common in the United States; for example, S. Typhimurium enteritis had been diagnosed in 600 persons in 44 states due to peanut butter contamination in 2008 (Maki, 2009). S. Typhimurium infection has also been often reported in China and was found to be the second most prevalent serotype (Ran et al., 2011).

Antimicrobial treatment is needed for infants, the elderly, and immunocompromised individuals with Salmonella infection. Fluoroquinolones and cephalosporins are the primary choice for clinical treatment (Glynn et al., 1998). In addition, azithromycin has gained the approval of the Food and Drug Administration (FDA) as an additional agent to treat Salmonella infections (Sjolund-Karlsson et al., 2011). With the extensive use of such antimicrobials, antimicrobial resistance is increasing at a serious rate in Salmonella isolates. In many countries, more and more Salmonella strains with MDR (defined as resistance to three or more classes of antimicrobials) have been discovered since the 1990's report of the spread of MDR in S. Typhimurium of definitive phage type 104 (DT104) in the world (Molbak et al., 1999). Relevant monitoring data showed that MDR in the entire Salmonella genus has increased from 20 to 30% in the early 1990s to 70% at the beginning of this century (Su et al., 2004). S. Typhimurium has also been found to show high rates of resistance to the traditional antimicrobials, and resistance to ciprofloxacin or cephalosporins have been found to have emerged in countries such as France and the United States (Weill et al., 2006; Whichard et al., 2007). A mass of S. Typhimurium isolates were also found to be resistant to ciprofloxacin or cephalosporins in many cities of China (Cui et al., 2008; Jiang et al., 2014). In recent years, some cases of azithromycin- resistance in patients with Salmonella infection were reported (Sjolund-Karlsson et al., 2011). Surprisingly, two strains have even been reported to be concurrently resistant to ciprofloxacin, cephalosporins, and azithromycin in China (Wong et al., 2014).

Shanghai is an economic and financial center located in eastern China and is divided into 16 administrative units with more than 24 million people. In order to better monitor public health issues, the Shanghai Center for Disease Control and Prevention (SCDC) became a member of the World Health Organization Global Food-borne Infections Network (WHO-GFN) in 2005 (Zhang et al., 2014). In this study, we aimed to analyze the antimicrobial resistance profiles of *S*. Typhimurium in Shanghai from 2011 to 2014 and tried to elucidate the molecular mechanisms underlying the emergence of MDR in these isolates. Our findings highlight the importance of increasing surveillance on these isolates with MDR, which will help provide appropriate clinical antimicrobial treatment for patients with *S*. Typhimurium infection.

MATERIALS AND METHODS

Specimen Collection and Isolate Identification

Fresh stool samples from clinically suspected patients who had diarrhea were collected from 24 sentinel hospitals and eight regional SCDC diagnostic laboratories in Shanghai as described previously (Zhang et al., 2014). The stool samples were then enriched in Selenite Brilliant Green broth (CHROMagar, China) for 16-22 h at 37°C. The enriched samples were then cultivated on Salmonella-Shigella (SS) agar or xylose lylose deoxycholate agar (XLD; CHROMagar, China) and incubated for 18-24 h at 37°C. Presumptive colonies were screened by testing in triple-sugar-iron agar, motility indole urea agar, L-lysine decarboxylase, and L-galactosidase (o-nitrophenyl-L-D-galactopyranoside; ONPG). One presumptive colony from each sample was stored in semisolid agar and sent to our laboratory for further confirmation. API 20E test strips (bioMerieux Vitek, Marcy-l'Etoile, France) were used to confirm the identity of the isolates. All the isolates were then serotyped by slide agglutination with commercial antiserum (S&A Reagents Laboratory, Thailand) according to the Kauffmann-White scheme (World Health Organization, 2011). This study was approved by Institute of Disease Control and Prevention, Academy of Military Medical Sciences (Beijing, China) and the informed consent was obtained from the subjects involved in this study.

Antimicrobial Susceptibility Testing

The minimum inhibitory concentrations (MICs) for 14 antimicrobial agents including cefoxitin (FOX), ceftriaxone (CRO), ceftiofur (XNL), azithromycin (AZI), chloramphenicol (CHL), tetracycline (TET), ciprofloxacin (CIP), gentamicin (GEN), nalidixic acid (NAL), sulfisoxazole (FIS), ampicillin (AMP), streptomycin (STR), amoxicillin/clavulanic acid at a 2:1 ratio (AUG2), and trimethoprim/sulfamethoxazole (SXT) were evaluated by broth microdilution using the Sensititre plate CMV3AGNF (Sensititre, Thermo Fisher Scientific, USA) according to the recommendations of the Clinical and Laboratory Standards Institute (CLSI) (Clinical Laboratory Standards Institute, 2016). An Escherichia coli ATCC 25922 strain was used for quality control.

PCR Amplification and DNA Sequencing

All the cephalosporin-resistant isolates were analyzed using PCR assays for the presence of extended-spectrum β -lactamase (ESBL) genes such as *bla*_{CTX-M} groups, *bla*_{OXA}, *bla*_{TEM}, *bla*_{SHV}, and *bla*_{CMY} (Hasman et al., 2005; Weill et al., 2006; Cui et al., 2015).

PCR amplification of quinolone resistance-determining regions (QRDRs) of gyrA, gyrB, parC, and parE (Giraud et al., 1999) and plasmid-mediated quinolone resistance (PMQR) determinants [qnrA, qnrB, qnrD, qnrS, and aac(6')-Ib-cr] (Park et al., 2006; Cui et al., 2015) were performed on the ciprofloxacin-resistant or intermediate resistant isolates. All azithromycin-resistant isolates were subjected to PCR to detect macrolide-resistance genes including mphA, mphB, ermA, ermB, ereA, mefA, and msrA (Phuc Nguyen et al., 2009). The primers used for the above mentioned PCR amplifications are shown in **Table 1**. All the PCR products were sequenced by the Beijing Genomics Institute (BGI). Sequences data were then analyzed by DNAstar (DNAstar Inc., Madison, WI, USA) and the sequences were compared with reference sequences from NCBI GenBank.

Statistical Analysis

Chi-squared test was used for data analysis using SPSS software (SPSS Inc., Chicago, IL, USA; version 17.0); a *P*-value < 0.05 was considered to indicate statistical significance.

RESULTS

S. Typhimurium Isolates from Human Patients in Shanghai, China, from 2011 to 2014

Between January 2011 and December 2014, 559 *S*. Typhimurium isolates were cultured from patients with diarrhea in Shanghai, China. The age of the patients ranged from 10 days to 86 years (19 cases unknown) (**Figure 1**). Children under 5 years of ages, and especially less than 1-year-old children, were highly susceptible to *S*. Typhimurium infection, which accounted for 49.4% of all the patients (P < 0.05). The ratio of the male to female patients was 1.3:1. Infections occurred mainly in summer and autumn (**Figure 1**).

Antimicrobial Susceptibility Testing

Among the 559 isolates, only 26 (4.7%) were susceptible to all 14 antimicrobials. Resistance to tetracycline was the most common (83.7%), followed by ampicillin (80.1%), nalidixic acid (79.2%), sulfisoxazole (77.1%), chloramphenicol (54.9%), streptomycin (53.7%), trimethoprim/sulfamethoxazole (47.4%), gentamicin (37%), and amoxicillin/clavulanic acid (7.9%) (**Table 2**). In addition, resistance to ceftiofur, ceftriaxone, and cefoxitin was found in 20, 20, and 5% of isolates, respectively. Notably, 3.6% (20/599) of the isolates displayed resistance (MIC $\geq 4 \ \mu g/mL$) to ciprofloxacin, and 9.1% (51/599) exhibited intermediate resistance to ciprofloxacin (MICs = $2 \ \mu g/mL$). More importantly, 22 of the isolates showed co-resistance to cephalosporins. Moreover, 31 (5.5%) isolates were showed resistance to azithromycin, and 6 of them were co-resistant to cephalosporins and ciprofloxacin.

Multidrug resistance was observed in 84.6% of the isolates, in which \geq 3, \geq 4, \geq 5, \geq 6, and \geq 7 classes of antimicrobials

were found in 84.6, 77.8, 61, 38.5, and 1.1% of the MDR isolates, respectively. Among the MDR isolates, 161 (28.8%) showed the ACSSuT resistance pattern (defined as resistance to ampicillin, chloramphenicol, streptomycin, sulfamethoxazole, and tetracycline); among them, 40 (7.2%) isolates exhibited reduced susceptibility to ciprofloxacin, 36 (6.4%) were resistant to cephalosporins, and 10 (1.8%) were resistant to azithromycin. It is noteworthy that 6 (1.1%) isolates with ACSSuT resistance pattern were concurrently resistant to ciprofloxacin and cephalosporins, and one of them was also co-resistant to azithromycin (**Table 2**).

PCR Detection of Antimicrobial Drug Resistance Genes and DNA Sequencing

Resistance genes including bla_{OXA} , bla_{TEM} , bla_{SHV} , bla_{CMY} , and bla_{CTX-M} in the 115 cephalosporin-resistance isolates were detected by PCR. PCR screenings revealed that 75 (65.2%), 52 (45.2%), 43 (37.4%), and 3 (2.6%) isolates contained the bla_{CTX} , bla_{TEM} , bla_{OXA} , and bla_{SHV} genes, respectively. All the strains were negative for bla_{CMY} . Fifty-two isolates contained two of the above described genes ($bla_{CTX-M}+bla_{TEM}/bla_{CTX-M}+bla_{OXA}/bla_{TEM}+bla_{SHV}$), and nine isolates concurrently contained bla_{CTX-M} , bla_{TEM} , $and bla_{OXA}$. Sequencing of the PCR products revealed that bla_{TEM-1} , bla_{OXA-1} , and bla_{SHV-12} were the main genotypes. bla_{CTX-M} included eight subtypes: $bla_{CTX-M-14}$, $bla_{CTX-M-123}$, and $bla_{CTX-M-125}$, $bla_{CTX-M-65}$, $bla_{CTX-M-14}$, $bla_{CTX-M-123}$, and $bla_{CTX-M-125}$, among which $bla_{CTX-M-14}$ and $bla_{CTX-M-55}$ were the most common subtypes (Figure 2).

We identified 71 isolates with decreased susceptibility to ciprofloxacin, and 65 of them contained at least one *gyrA* mutation which mainly occurred at encode 87 (D87Y, D87N, or D87G). Among them, six had double mutations (S83F/D87N or D87G) in the *gyrA* gene and a single mutation (S80R) in the *parC* gene; 1 isolate with four mutations, including two in *gyrA* gene (S83F/D87N) and two in *parC* gene (T57S/S80R); 58 isolates with only one *gyrA* mutation (D87Y or D87N). No point mutations in *gyrB* and *parE* were found. Here, three species of PMQR determinants including *aac*(6')-*Ib*-*cr* (n = 50), *qnrB* (*qnrB2*, n = 2; *qnrB4*, n = 4), and *qnrS1* (n = 1) were detected. Among the 49 isolates with no mutation or only one mutation in *gyrA* gene, one or two PMQR genes were detected (**Table 3**).

In addition, PCR results showed that 15 out of the 31 azithromycin-resistant isolates (MIC \geq 128 µg/mL) harbored *mphA* genes, while the other 16 (MIC: 16–64 µg/mL) did not. All the azithromycin-resistant isolates were negative for *mphB*, *ermA*, *ermB*, *ereA*, *mefA*, and *msrA*.

Notably, among the 22 isolates that concurrently exhibited reduced susceptibility to cephalosporins and ciprofloxacin, 15 contained ESBL and PMQR genes. Two isolates contained four types of antimicrobial-resistance genes: $qnrB/aac(6')-Ib-cr/bla_{\text{CTX-M}}/bla_{\text{TEM}}$ (n = 1) and $aac(6')-Ib-cr/bla_{\text{CTX-M}}/bla_{\text{TEM}}$ (n = 1). Nine isolates harbored three types of antimicrobial resistant genes, including $qnrB/aac(6')-Ib-cr/bla_{\text{OXA}}$ (n = 2), $aac(6')-Ib-cr/bla_{\text{OXA}}/bla_{\text{CTX-M}}$ (n = 4), and $aac(6')-Ib-cr/bla_{\text{CTX-M}}/bla_{\text{TEM}}$ (n = 3). Four

TABLE 1 | Primers for the PCR detection of antimicrobal-resistance determinants.

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| blamba PATAAAATTCTTGAAAGAQAAA 1080 Weill et al., 2006 RGACAGTTAGCCAGTTAGCCACC 795 Weill et al., 2006 RGATTGGTGATGCQGCGGCGTACC RGATTGGTGATGCQGCGGCGGCG RGATTGGGTGAGCCGGGCGGGCG RGGTCGAGCCGGGGCGTGTGTGAA ARGGTCGGGCGGGCGGGGCG RGGTCGGGGCGGGGGGGGG RGGTCGGGGGGGGGGGGGGGG RGGTGGTGGGGGGGGGGGGGGG | | R:AATTTAGTGTGTTTAGAATGG | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Reaceastructoratitaccoastructoratitaccoastructoratitaccoastructoratitaccoastructoratitaccoastructoratita | bla _{TEM} | F:ATAAAATTCTTGAAGACGAAA | 1080 | Weill et al., 2006 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| bleyw FITACTOCCUTGTAGCCACC 796 Weill et al., 2006 RGATTIGGTGAATGCCAGCATC 195 Hasman et al., 2006 RGATCIGGTGAGCCAGCATC 195 RGATCIGGGAGCCAGCATC 195 RGATCIGGGAGCCAGCAGCA 195 RGATCIGGGCAGCGAGCAGCA 197 RGATCIGGCGCAGGAGCA 197 RGATCIGGCGCAGGCAGAGCG 197 RGATCIGGCGCAGGCGGAA RGATCIGGCGAGGCGGAAGCG 197 RGATCIGGCGCAGGCGGAAGCG 197 RGATCIGGCGCATGCGCAGAGCG 197 RGATCIGGCGCATGCGCAGAGCG 197 RGATCIGGGCGATGGCGAAGCG 298 RGATCIGGGCATAGCGCAGGCGG RGATCIGGCGCATAGCGGCAGGCG RGATCIGGCGCATAGCGGCAGGCG RGATCIGGGCATAGCGCAGGCG RGATCIGGGCATAGCGCAGGCG RGATCIGGGCATAGCGCAGGCG RGATCIGGGCATAGCGCAGGCG RGATCIGGGCAGAGCGG RGATCIGGGCAGAGCG RGATCIGGGCAGAGCG RGATCIGGGCAGAGCG RGATCIGGGCAGAGCG RGATCIGGGCAGAGCG RGATCIGGGCAGGCTAGCA RGATCIGGGCAGGCTAGCA RGATCIGGGCAGGCTAGCA RGATCIGGGCAGGCTAGCA RGATCIGGGCAGGCTAGCA RGATCIGGGCAGGCTAGCA RGATCIGGGCAGGCTAGCA RGATCIGGGCAGGCTGGCGA RGATCIGGGCAGGCTGGCGCA RGATCIGGCGCGGCGCAGA RGATCIGGCCGGGCGCTG RGATCIGGCGCGGCGCTG RGATCIGGCGCGGCGCTG RGATCIGGCGCGGCGCTG RGATCIGGCGCGGGCGCGCGCGC RGCGCGTGGCGCGCGCGCGCG RGATCIGGCGGCGGCGCGCGCGCGCG RGCGCCTGGCGGCGCGCGCGCGCGC RGCGCCTGCGGCGCGCGCGCGC RGCGCCTGCGGCGCGCGCGCGC RGCGCCTGCGGCGCGCGCGCGC RGCGCCTGCGGCGCGCGCGCGCGC RGCGCCTGCGGCGCGCGCGCGCGCGCGC RGCGCCGCGCGCGCGCGCGCGCGCGCC RGGCCGCCGCGCGCGCGCGCGCGCGCGCGCC RGGCCGCCGCGCGCGCGCGCGCGCC RGGCCGCCGCGCGCGCGCGCGCGCC RGGCCGCCGCGCGCGCGCGCGCGCC RGGCCGCCGCGCGCGCGCGCGCGCGCGCGCGCGCGCGCG | | R:GACAGTTACCAATGCTTAATC | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Rightmodified Rightmodified Part of the second of the sec | bla _{SHV} | F:TTATCTCCCTGTTAGCCACC | 795 | Weill et al., 2006 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| bit RGGTGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGG | | R:GATTTGCTGATTTCGCTCGG | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| R-GGTCGAGCCGGTCTTGTGAA A GRDR of Topoisomerase genes F: GGGCAATCACTGGAACCA 431 This study gy/A F: GGGTGATGGCGGGGGATA | bla _{CMY} | F:GTGGTGGATGCCAGCATCC | 915 | Hasman et al., 2005 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| grAF1 GGGCATGAGACTGGAAGAG431This studyre GGTTGTCGGCGGGGATARCGTGTCGGCGGGGATA309Cul et al., 2015grBRCGTGTCATTAGCAGAGCG309Cul et al., 2019parCRTGACGCAGTGTGGCTAAAGAG90Cul et al., 2016parGRTGACGCAGTGCGGCTAAAAAGTG90Cul et al., 2016parGARTGACGCAGTGCGGCTAAAAAGTG90Cul et al., 2016parGARTGACGCAGTGCGGCTAAAAAGTG90Cul et al., 2016parGARTGATGCGCGAAGGTTAGGTAACAG516Cul et al., 2016qrAAPATGCGCGGCAAAGGTTAGGTCA100100qrAAPCGATGGTGAAAGCCAAAAAGGTA656Cul et al., 2015qrABFCGATGGTGAAAGCCGAAAAGGTAGGCCG100et al., 2016qrADPCGAGAGTCATGTCAGCAACGCAA417Cul et al., 2016qrACAPCGAGAGTCGTCAACTGCGCAA412016qrADPCGAGAGTCGTAAGTGGCTAA420Pack et al., 2006qrADPCGAGAGTCGTAAGTGGCTAACTGCGCAAC420Pack et al., 2006qrADPCGAGAGTCGTAAGTGGCGAACTGCGCAGGTGTTT100100qrADPCGAGAGTCGTAAGTGGCAACTGGCAGGTGT100100qrADPCGAGAGTCGTAACTGCCCAAG494Phuc Nguyen et al., 2009RCGCTCTATCACACTGCATGCAGGACTGGCAGGTGGC100Phuc Nguyen et al., 2009qrADPCGAGATCTATAACCACATATACAAAATAG494Phuc Nguyen et al., 2009RCGCCTTACTGCACTGCAGGCTGGAGGCTGGAGGCTGGAGGCTGGAGGCTGGGGGGTCATGGACTGTATGGGGTCATGGAGCCTGTAGGACTGCTATGGGGTCATGGAGCTGGGGGCT100qrAD | | R:GGTCGAGCCGGTCTTGTTGAA | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| gyrAF: TGGGCAATGACGGGAACA431This studygyrB:: GGTTGTGCGCGGGATA00Oui et al., 2015gyrB:: FATGACGGATTGGCAGAGCG00Oui et al., 2015parC:: FATGACGGATTGGCAGAGCG290Oui et al., 2015parG:: FATGACGGATTGGCAGAGCG290Oui et al., 2015parG:: FATGACGGGCTGCGGGCTAAAAAGTG290Oui et al., 2015parG:: FATGCGGTGCGGGCTAAAAAGTG290Oui et al., 2015parG:: FATGCGGGCAGGATTG516Cui et al., 2015mTG <td:: sgatggggaaggccagaagg<="" td="">469Oui et al., 2015gmB<td:: sgatggggaaggccagaaagg<="" td="">469Oui et al., 2015gmGA<td:: sgatggggaaggccagaagg<="" td="">417Oui et al., 2015gmGA<td:: sgatgggggaata<="" td="">666Oui et al., 2015gmGA<td:: sgagggggggata<="" td="">417Oui et al., 2015gmGA<td:: sgagggggggggggggggggggggggggggggggggg<="" td=""><td>QRDR of Topoisomerase genes</td><td></td><td></td><td></td></td::></td::></td::></td::></td::></td::> | QRDR of Topoisomerase genes | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| P: GGTGTGGGGGGGATAgyrBF: ATGAGCGATATGGCAGAGGG309Oil et al., 2015parCF:ATGAGCGATATGGCAGAGGG413Giraud et al., 1999ParGF:ATGAGCGGTAAAAAGTGG290Oul et al., 2015parEF:ATGCGTGGCGGCGGAAAAAGTG290Oul et al., 2015parEF:ATGCGTGGCGGCGGAAAAAGTGGATAC700001 et al., 2015PMCRF:GCGTGGCAGGATTGGCAGAC700011 et al., 2015qmBF:GATCGTGGAAAGGTTGGTGA469Cui et al., 2015qmBF:GATCGTGGAAAGCCAGAAAGG469Cui et al., 2015qmBF:GGAGGCAGGAATTGTCC700700qmCF:GGAGGCAGGGGATA417Cui et al., 2015qmBF:GGAGGTGAAAGCCGGAAAGGGGCCTG700700qmBAF:GGAGGTGCACTGGCAATA417Cui et al., 2015qmACF:GGAGGTGCTGTAGGCTA482Park et al., 2006qmDAF:GTGAGGGGGGGGGTGT700700qmBAF:GTGAGGGGGGAGCTTGGGGGG403Phuc Nguyen et al., 2009qmACF:GTGAGGGGGGAGCTTGGGGAG494Phuc Nguyen et al., 2009qmAAF:GTGAAAGCATGGACTGGGGAGG494Phuc Nguyen et al., 2009qmAAF:GTGAAAGCATGGAGAGGGGGGGGG700700qmAAF:GGAGGGGGGAGCTGGGGAGGG700700qmAAF:GGAGGGGGGGAGCTGGGGAGGG700700qmAAF:GGAGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGGG | gyrA | F: TGGGCAATGACTGGAACA | 431 | This study | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| gyrBF: ATGAGGGATATGGGAGAGGG309Cui et al., 2015R:GCTGTGATAACGAGATTTGTCCGGGF:Giraud et al., 1999parCF:ATGAGCGATTGGCGTAACAGG413Giraud et al., 1999parBF:ATGAGCGATTGGCGTAACAGG280Cui et al., 2015parBF:ATGGCGGGGTGCAGGATGGATCG516Cui et al., 2015parBF:ATTGCGGCAGGGAAGGATGGA516Cui et al., 2015qmAF:ATGGCGAAGGCAGAAAGG469Cui et al., 2015qmBF:GATCGTGAAAGCCAGAAAGG469Cui et al., 2015qmBF:GATCGTGAAAGCCAGAAAGG417Cui et al., 2015qmBF:AGGACGTGAAAGCGCAGAAAGG417Cui et al., 2015qmSF:AGGACGTGAACGCGCAGA417Cui et al., 2015qmSF:AGGACGTGAGCGGCATA417Cui et al., 2015qmSF: <tgcgatgctcttggggcaactgcaca< td="">417Cui et al., 2006qmSF:<tgcgatgctcttggggcacatggcaca< td="">417Cui et al., 2006qmAF:<tgcgatgcctcttggggcaca< td="">412Pink et al., 2006qmAF:<tgcgatgcctcttggggcaga< td="">413Pink et al., 2009qmAF:<tgcgatgcctcttggggcaga< td="">413Pink et al., 2009qmAF:<tgcgccaggagcctcggcaggc< td="">494Pink et al., 2009qmAF:<gctaatgcaccatggaagaa< td="">533Pink Nguyen et al., 2009qmAF:<gctaatgctcaaccgaaagga< td="">533Pink Nguyen et al., 2009qmAF:<gcaaacttatgcgagaacttaacgagagc< td="">420Pink Nguyen et al., 2009qmAF:<gcacatactttttggggtcatgaagggc< td="">420Pink Nguyen et al., 2009<td></td><td>R: GGTTGTGCGGCGGGATA</td><td></td><td></td></gcacatactttttggggtcatgaagggc<></gcaaacttatgcgagaacttaacgagagc<></gctaatgctcaaccgaaagga<></gctaatgcaccatggaagaa<></tgcgccaggagcctcggcaggc<></tgcgatgcctcttggggcaga<></tgcgatgcctcttggggcaga<></tgcgatgcctcttggggcaca<></tgcgatgctcttggggcacatggcaca<></tgcgatgctcttggggcaactgcaca<> | | R: GGTTGTGCGGCGGGATA | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| RGCTGTGATAAGGCAGTTTGTCCGGGG parC F:ATGAGCGATATGGCAGAGCG 413 Giraud et al., 1999 parE F:ATGGTGCGGCGCGCAAAAGGT 290 Cui et al., 2015 parE F:ATGGTGCGGCGCGCAAAAAGTA 290 Cui et al., 2015 parC F:ATTGCTCACGCCAGGATTAG 290 Cui et al., 2015 PMOR F:ATTCTCACGCCAGGAAAGGTAGGTCA 200 Cui et al., 2015 garA F:ATTCGTCACGCCAGGAAAGG 469 Cui et al., 2015 garA F:AGTCGTGAAAGCCAGAAAAGG 469 Cui et al., 2015 garA F:AGAGCGCGCTGGTAGTGTTGTCC GarAACAGCCCGTGTGTAGTGTCC GarAACAAGCTGAAAGCCCCTGTAAGCCAGGAATA 656 Cui et al., 2015 garA F:AGAGACATCGGTGAACTGGCAA 417 Cui et al., 2015 garA F:AGAGACATCGTGAACGTGAAAGGTAACAGCACTGTAGGC 482 Park et al., 2006 garCGCTATAGGCAGAGCTTGGAGGGTA 482 Park et al., 2009 Proceaga CGCCTATAGGCTGGAGGTC garA F:GTGAAGGCAGCTGGAGAGCTTCGGAGGGT F:GTGAGAGACATGGAAAGAAAA 533 Phuc Nguyen et al., 2009 garCTTACCGATACCGTAAAAGGAGCACTTAAAAGAAA 533 Phuc Nguyen et al., 2009 <td>gyrB</td> <td>F: ATGAGCGATATGGCAGAGCG</td> <td>309</td> <td>Cui et al., 2015</td> | gyrB | F: ATGAGCGATATGGCAGAGCG | 309 | Cui et al., 2015 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| parC FATGAGCGATATGGCAGAGCG 413 Giraud et al., 1999 RTGACCGAGTTGGCTTAACAG Cui et al., 2015 Cui et al., 2015 ParE FATGGTGCGCGAGAGGGT S0 Cui et al., 2015 PMOR FATTGTCACGGCAGAAGGTTAGGTCA S16 Cui et al., 2015 grirA FATTGTCACGCCAGGAATGG 469 Cui et al., 2015 grirB F:GATCGTGAAAGCCAGAAAGG 469 Cui et al., 2015 grirB F:GATCGTGAAAGCCAGAAAGG 469 Cui et al., 2015 grirB F:GATCGTGAAAGCCAGAAAGG 469 Cui et al., 2015 grirB F:GATCGTGAAAGCCCGGAAAGG 469 Cui et al., 2015 grirB F:GATCGTGAAAGCCCGGAACGG 417 Cui et al., 2015 grirB F:GACGACTGCACCGGAGGCTG 42 Park et al., 2006 grirB F:GATGATGCAGCCGGAGGCTGCCGAAG 417 Cui et al., 2009 grirB F:GTGAGAGAGGAGCTGCCGGAGGCT 403 Phuc Nguyen et al., 2009 grirB F:GTGAGGAAGGAGGAGCTCGCGAGG 403 Phuc Nguyen et al., 2009 grirB F:GTGAGAAGGAGCTGACCAGGAGGTCCCCAAGA 53 | | R:GCTGTGATAACGCAGTTTGTCCGGG | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| R:TGACCGAGTTOGCTTAACAGparEF:ATGCGTGCGGCTAAAAAAGTG290Cui et al., 2015PMORR:TGGTGGCGGCAGAGATTG516Cui et al., 2015qmAF:ATTTGCACGGCAAGGATTGG516Cui et al., 2015qmBF:GATCGTGAAAGCCAGGAAAGG469Cui et al., 2015qmCF:GATGGGAAAGCGGGGAATTA656Cui et al., 2015qmCF:GGAGATCAATTACGGGGAAATA656Cui et al., 2015qmSR:ACGATGCCTGTAGTGTCC7Cui et al., 2015qmSF:ACGAGTCCATTACGGGAAATA656Cui et al., 2015qmSR:ACAAGCGTGAGGCCTG3417qmSR:ACCAATGCTGAGGCCTG3411qmSR:TGCGAATGCTCTATGAGTGGCTA482Park et al., 2006qmSR:TGCGAAGCCTCGTAGGGCTG482Park et al., 2006qmpAR:TGCGCAGGAGCTCGCGGAG403Phuc Nguyen et al., 2009qmpAR:GGCGCAGGACTCGCGGAG403Phuc Nguyen et al., 2009qmpAR:GGCGCAGGACTCGCGGAGGTC494Phuc Nguyen et al., 2009qmAR:GGCTATATAAACGAGTATAAAGAAA533Phuc Nguyen et al., 2009qmAR:GGCGATGTATAAAGCAGTTAAAAGAAA533Phuc Nguyen et al., 2009qmAR:GCCGGTGTCTATGAGCCTTGCemAPhuc Nguyen et al., 2009qmAR:GCCGGTGTCTAGACTTAGAGC420Phuc Nguyen et al., 2009qmAR:GCCGGTGTCTAGACTTAGAGC420Phuc Nguyen et al., 2009qmAR:GCCGGTGCTCATGAGCTGGAGGGCT455Phuc Nguyen et al., 2009qmAR:GCCGGTGCTCATGAGCTGGAGGGC450 | parC | F:ATGAGCGATATGGCAGAGCG | 413 | Giraud et al., 1999 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| parE F.ATGCGTGCGGCTAAAAAAGTG 290 Cui et al., 2015 PMOR | | R:TGACCGAGTTCGCTTAACAG | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| R:TCGTCGCGCTGTCAGGATCGATAC PMOR grt7A F:GATCGTCGCAGAGGTTTAGGTCA grt7B F:GATCGGCAAAGGTTAGGTCA grt7B F:GATCGTGAAAQCCAGAAAGG 469 Cui et al., 2015 grt7D F:GACGATGACTGTTGTCC Ui et al., 2015 grt7D F:CGAGACTCATTTACGGGGAAATA 656 Cui et al., 2015 grt7D F:CGAGACTCATCTCACACTGCAACTGCAAC 417 Cui et al., 2015 grt7C F:ACGATCGCTCTATGAGCGCCTG ac(6')-l/b-cr F:TGCGATGCTCTATGAGTGGCTA 482 Park et al., 2006 grt7A F:TGCGATGCTCTGTAGAGGGCTA 482 Park et al., 2006 ac(6')-l/b-cr E:TGGAGAGGCTCGGCAGGACTCGGCAGG 403 Phuc Nguyen et al., 2009 grt7A F:GCGCGCAGGACTCGGCAGGTC mphA F:GCGCGCAGGACTCGGCAGGTC mphA Phuc Nguyen et al., 2009 grt7C F:GCCGCAGGACTCGCCAAGG 494 Phuc Nguyen et al., 2009 Phuc Nguyen et al., 2009 grt7A F:GCGATGCTGTAAAAGGATGTAAAAGAA 533 Phuc Nguyen et al., 2009 grt7C F:GCCGGTGCTCAACCAAATA 693 Phuc Nguyen et al., 2009 grt7A F:GCCGGTGCTCATGAGAGCTC met Al., 2009 Phuc Nguyen et al., 2009 | parE | F:ATGCGTGCGGCTAAAAAGTG | 290 | Cui et al., 2015 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| PMOR FLATTICTOCAGCCAGGATTG 516 Cui et al., 2015 gnrA FLATTICTOCAGCCAGAAAGGTA 669 Cui et al., 2015 gnrB FLGATCGTGAAAGCCCAGAAAGG 656 Cui et al., 2015 gnrD FLGAGACATCTGTCAGCCCGG Cui et al., 2015 gnrD FLGGAGATCGTGTAAGCGCCGG Cui et al., 2015 gnrS FLGGGAGTCGCTGGCAAGCGCCGG Cui et al., 2015 gnrS FLGGGAGTCGCCTGTGAGGCGCTG Cui et al., 2015 gnrS FLGGGAGTCGCCTGTGAGGGCCTA 482 Park et al., 2006 gnrS FLGGGAGGCCTGGGGGGGCTA 482 Park et al., 2006 gnrS FLGGAGGAGGAGCTCGGGAGGTC Phuc Nguyen et al., 2009 gnrGCCTGTAGGGGGAGGTC FLGGAGAGGAGCTCGGAGGGTC Phuc Nguyen et al., 2009 gnrBA FLGCGAGAGGACTCGGAGAGTC Phuc Nguyen et al., 2009 gnrBA FLGCTAAGTGTAAAGGAGAGTCGCAGAG Phuc Nguyen et al., 2009 gnrBA FLGCGAGGCTCTAAGGAGAGACTCGAGAGAGC Phuc Nguyen et al., 2009 gnrBA FLGCTAAGTGTAAAGGTAAAGAA Phuc Nguyen et al., 2009 gnrBA FLGCATAGTGTAAAGGTAACGAGAATAG Phuc Nguyen et al., 2009 gnrGGGGGCGCTATGAGGCGCTTACCAGAGAGC FLGGAGAGCTCTACCAGAG | | R:TCGTCGCTGTCAGGATCGATAC | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
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| gnrBF:GATCGTGAAAGCCAGAAAGG469Cul et al., 2015R:ACGATGCCTGGTAGTTGTCCF:CGAGATCAATTACGGGGAATA656Cul et al., 2015gnrDF:ACGACGTCGCCAACTGGCAACTGGCAA417Cul et al., 2015mrSAF:ACGACGTCGTCAACTGGCAAC482Park et al., 2006acc(6) / b/- crF:TGCGATGCCTGTAGAGTGGCTA482Park et al., 2006mrSAF:GCGATGCTCTATGAGTGGCTG482Park et al., 2006mrAATTGGCAACTGGCAGGGTGTTTF:TGCGATGCCTGGCGGTGTTTF:TGCGATGCCTGGCGGGGTGTTTMarcolide-resistance GenesmphAF:GTGAGGAGGAGCTTCGCGAG403Phuc Nguyen et al., 2009mphBF:GCCGCAGGACTGGGAGGGTCF:GCCGCAGGACTGCGAGGGTCF:GCCGCAGGACTGCGAGGGTCmphBF:TCTTATAAGACAGTATACAGAATAAG533Phuc Nguyen et al., 2009mrGCGTTATTTTTGTGATCCTTCF:GCATATTTTTTGTAGTCCTTCF:GCATATTTTTTGTAGTCCTTCerrAF:GCCGGTGCTCATGAACAGTAATAAGAA633Phuc Nguyen et al., 2009mrAAF:GCCGGTGCTCATGAACAGTGTAAAGGAA533Phuc Nguyen et al., 2009mrAAF:GCCGGTGCTCATGAACTTGAG420Phuc Nguyen et al., 2009mrAAF:GCCGGTGCTCATGAACTTGAGG420Phuc Nguyen et al., 2009mrAAF:GCCGTGCTCATGAACTTGAGGF:GCACTTATTGCGTCAGAGGCmrAAF:GCCGTGCTCATGAACTTGATCGCAGAGGCF:GCACTTATTGCGTCATGAGGGGTmrAAF:GCCGTTGCTCATTAGTCGATAAGGGG345Phuc Nguyen et al., 2009mrAAF:GCTATTAGTGCTGATGAAGGGGTAGGGGGTAGGGF:GCTATTAGTCATAAGTCATGAGGGmrAAF:GCATTATTGGGTGCTGATGAAGGGGGTAGGGGGGGGGGG | | R:GATCGGCAAAGGTTAGGTCA | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| R:ACGATGCCTGGTAGTTGTCCgnrDF:CGAGATCATTTACGGGGAATA656Cui et al., 2015R:AACAAGCTGAAGCGCCTGR:AACAAGCTGAAGCGCCTGIIIIIIIIIIIIIIIIIIIIIIIIIIIIIIIII | gnrB | F:GATCGTGAAAGCCAGAAAGG | 469 | Cui et al., 2015 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| qnrDF:CGAGATCAATTTACGGGGAATA656Cui et al., 2015R:ACAAGCTGAAGCGCCTGR:ACGACATTCGTCAACTGCAA417Cui et al., 2015qnrSF:ACGACATTCGTCAACTGCAA482Park et al., 2006aca(6')-lb-crR:TGCGATGCTGAGGGCTG482Park et al., 2006aca(6')-lb-crR:GCTGGAGGGAGGCTTCGCGAG403Phuc Nguyen et al., 2009mphAF:GTGAGGAGGAGCTTCGCGAGG403Phuc Nguyen et al., 2009mphBF:GTAATTAAACAAGTAATCAGAATAG494Phuc Nguyen et al., 2009mrAF:GTCTAAAAGCATGTAAAAGAAA533Phuc Nguyen et al., 2009mrAF:GCAGTACTTTGTAGTCCATACGsereesereeermAF:GCCGTGCTCATGCAACTACG693Phuc Nguyen et al., 2009mrAF:GCCGTGCTCATGCAACTGAACTGCAAATA693Phuc Nguyen et al., 2009mrAF:GCCGTGCTCATGAACTTGAGGCsereesereemrAF:GCCGGTGCTCATGAACTTGAGG420Phuc Nguyen et al., 2009mrAF:GCCGTGTCCTGTAGACTTGAGGCsereesereemrAF:GCCGGTGCTCATGAACTTGAGGsereesereemrAF:GCCGGTGCTCATGAACTTGAGG420Phuc Nguyen et al., 2009mrAF:GCCGTGTCCTATGCAGAGGCsereesereemrAF:GCCGGTGCTCATGAACTTGAGGsereesereemrAF:GCCGTGTCCTGAGAACTTGAGGsereesereemrAF:GCCGGTGCTCATGCAGAGGCsereesereemrAF:GCCTTATCGGAGTAGTGGsereesereemrAF:GCCTATAGCTCATCGTGsereesereemrAF:GCCTTATCGGGG | | R:ACGATGCCTGGTAGTTGTCC | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| R:AACAAGCTGAAGCGCCTGqnrSF:ACGACATTCGTCAACTGCAA417Cui et al., 2015 R:TAAATTGGCACCCTGTAGGCaac(6')-lb-crF:TTGCGATGCTCATGAGTGGCTA482Park et al., 2006 R:CTCGAATGCCTGGCGTGTTTMacrolide-resistance GenesmphAF:GTGAGGAGGAGCTCGGGAGGTC403Phuc Nguyen et al., 2009 R:GCGCCAGGACTCGGAGGGTCmphBF:GGTGAGGAGGACTCGGAGGGTCmphBF:GGTGAGGAGCTCGGAGGACT494Phuc Nguyen et al., 2009 R:GCTCTTACTGCATCCATACGermAF:TCTAAAAAGCATGTAAAAGAAA533Phuc Nguyen et al., 2009 R:GCATCTTTTGTAGTCCTTCermBF:GAAAAAGCATGTAAAAAGAAA533Phuc Nguyen et al., 2009 R:CGACTCTATGAGACCCATACGereAF:GGCGGTGCTCATGAACCAAATA693Phuc Nguyen et al., 2009 R:CGACTCTATCGACCATACGmarAF:GGCAGTGCTCATGAACTTGAG420Phuc Nguyen et al., 2009 R:CGACTCTATCGATCAACGAGGCmarAF:GCACTCATTCGATCAACCAAATA693Phuc Nguyen et al., 2009 R:CGACTCTATTGATCAGAGGCmarAF:GCCACTCATTGAGCACGAGGCmarAmarAF:GCCACTCATTGAGCAGAGGCmarAmarAF:GCACTCATTGAGCACGAGGCmarAmarAF:GCACTTATTGGGGGTACTAGGG384marAF:GCTATAAGTGCCTGTGCGTG842marAF:GCTATAAGTGCCTGTGGG1000 Pinc Nguyen et al., 2009 R:GTCTATAAGTGCGTGATGGTGmarAF:GCACTTATTGGGGGTAATGGG384marAF:GCTATTAAGTGCCTGTGGGGmarAF:GCTATTAAGTGCCTGTCGTGmarAF:GCTATTAAGTGCTCTGCGGGmarAF:GCACTTATTGGGGGTAATGGG< | gnrD | F:CGAGATCAATTTACGGGGAATA | 656 | Cui et al., 2015 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| qn/SF.ACGACATTCGTCAACTGCAA417Cui et al., 2015B:TAAATTGGCACCCTGTAGGCB:TAAATTGGCACCCTGTAGGCB:CTCGAATGCCTGACGGCTA482Park et al., 2006acc(6')-lb-crF:TGCGATGCTCTATGAGTGGCTA482Park et al., 2006B:CTCGAATGCCTGGCGTGTTTB:CTCGAATGCCTGGCGAGGTCCCmphAF:GTGAGAGGAGCTTCGCGAGG403Phuc Nguyen et al., 2009B:TGCCGCAGGACTCGGAGGTCB:TGCCGCAGGAGTCCCmphBF:GATATTAAACAAGTAATCAGAATAG494Phuc Nguyen et al., 2009B:GCTCTTACTGCATCCATACGB:GCGATACTTTTTGTAGTCCATACGCemAF:GCAAAAGTACTCAACCAAATA693Phuc Nguyen et al., 2009B:GCGTTATTGGATCCAACCAAATA693Phuc Nguyen et al., 2009B:GCGGTGGTCATGAACTTGAGCCCereAF:GCGGGTGGTCATGAACAGGCCmefAF:AGATCATTAATCACTAGTGC340mefAF:AGATCATTAACTAAGTGGCSmsrAF:GCACTTATTGGGGGTAATGGA344Phuc Nguyen et al., 2009B:TCTCTGGGGTAATGGGB:TCTTCTGGGGTAATGGAGGGCSPhuc Nguyen et al., 2009B:TCTTCTGGTACTAAAGTGGCSPhuc Nguyen et al., 2009B:TCTTCTGGTACTAAAGTGGCSPhuc Nguyen et al., 2009B:TCTTAAGTGCTCATGAGGGCSPhuc Nguyen et al., 2009B:TCTTAAGTGCTCATGAGGGCSPhuc Nguyen et al., 2009B:TCTTAAGTGCTCATGAGGGCSPhuc Nguyen et al., 2009B:TCTTAAGTGCTATAGTGGTACTAAAAGTGGSPhuc Nguyen et al., 2009B:TCTTAAGTGCTATAAGTGAGGGCSPhuc Nguyen et al., 2009< | | R:AACAAGCTGAAGCGCCTG | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| R:TAAATTGGCACCCTGTAGGCaac(6')-lb-crF:TTGCGATGCTCATGAGTGGCTA482Park et al., 2006R:CTCGAATGCCTGGCGTGTTTR:CTCGAATGCCTGGCGAGGTC403Phuc Nguyen et al., 2009Macrolide-resistance GenesR:TGCCGCAGGAGCTCGGCAGG403Phuc Nguyen et al., 2009mphAF:GTGAGGAGGAGCTCGGAGGTC494Phuc Nguyen et al., 2009mphBF:GATATTAAACAAGTAATCAGAATAG494Phuc Nguyen et al., 2009R:GCTCTTACTGCATCCCATACGemAF:TCTAAAAAGCATGTAAAAGAAA533Phuc Nguyen et al., 2009R:GCTATTTGTAGTCCTTCemBF:GAAATAGTACTCAACCAAATA693Phuc Nguyen et al., 2009R:AATTTAAGTACCGTTACTereAF:GCGGTGGTCATGAACTTGAG420Phuc Nguyen et al., 2009R:CGACTCTATTCGGTCATGAGGGGmefAF:GCACTCTATTGGTGCCATAGGGCmsrAF:GCACTTATTGGGGGTAATGG345Phuc Nguyen et al., 2009R:GTCTTATGGGAGTAATGGGmsrAF:GCACTTATTGGGGGTAATGG345Phuc Nguyen et al., 2009R:GTCTATAGGGGGTAATGGmsrAF:GCACTTATTGGGGGTAATGG384Phuc Nguyen et al., 2009R:GTCTATAGGGGCTAATGGGmsrAF:GCATTATGGGGGTAATGGR:GTCTATAGGGGCTAATGGGMarcolideMarcolideMarcolide <td< td=""><td>gnrS</td><td>F:ACGACATTCGTCAACTGCAA</td><td>417</td><td>Cui et al., 2015</td></td<> | gnrS | F:ACGACATTCGTCAACTGCAA | 417 | Cui et al., 2015 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| aac(6')-lb-cr F:TGCGATGCTCTATGAGTGGCTA 482 Park et al., 2006 R:CTCGAATGCCTGGCGTGTTT Marolide-resistance Genes mphA F:GTGAGGAGGAGCTTCGCGAG 403 Phuc Nguyen et al., 2009 R:TGCCGCAGGACTCGGAGGTC mphB F:GATATTAACAAGTATCAGAATAG 494 Phuc Nguyen et al., 2009 R:GCTCTTACTGCATCCATACG ermA F:TCTAAAAGCATGTAAAAGAAA 533 Phuc Nguyen et al., 2009 R:CGATACTTTTGTAGTCCTTC ermB F:GAAAAAGTACTCAACCAAATA 693 Phuc Nguyen et al., 2009 R:CGATACTTAAGTACCTAACGAATAG 420 Phuc Nguyen et al., 2009 R:CGATCCTATCGATCCAACCAAATA 693 Phuc Nguyen et al., 2009 R:CGATCCTATCGATCCAACCAAATA 693 Phuc Nguyen et al., 2009 R:CGATCTCATTCGATCCAACCAAATA 693 Phuc Nguyen et al., 2009 R:CGATCTCATTCGATCCAACCAAATA 693 Phuc Nguyen et al., 2009 R:CGACTCATTCGATCCAGACCTAACGAACT ereA F:GCCGGTGCTCATGAACTGAACTGAACTGAAC R:CGCACTCATTCGATCCAGAGGC mefA F:AGTACATTAATCACTAGTGC 345 Phuc Nguyen et al., 2009 R:CTCTTCTGGGTACTAAAAGTGG marA | | R:TAAATTGGCACCCTGTAGGC | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
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| Macrolide-resistance Genes F:GTGAGGAGGAGCTTCGCGAGG 403 Phuc Nguyen et al., 2009 mphA F:GCTGAGGAGCATCGGAGGTC 494 Phuc Nguyen et al., 2009 mphB F:GCTTTACTGCATCCGTACG 494 Phuc Nguyen et al., 2009 ermA F:TCTAAAAAGCATGTAAAAGAAA 533 Phuc Nguyen et al., 2009 R:CGATACTTTTTGTAGTCCTTC F:GCAAAAGTACTCAACCAAATA 693 Phuc Nguyen et al., 2009 ereA F:GCAGGTGCTCATGAACTTAGG 420 Phuc Nguyen et al., 2009 rerA F:GCCGGTGCTCATGAACTTAGG 420 Phuc Nguyen et al., 2009 rerA F:GCCGGTGCTCATGAACTTAGG 420 Phuc Nguyen et al., 2009 rerA F:GCCGGTGCTCATGAACTTGAGGC Phuc Nguyen et al., 2009 rerA F:GCCGTTGCTCATGCAACCGAAGGC Phuc Nguyen et al., 2009 mefA F:AGTATCATTAACCATGTGC 345 Phuc Nguyen et al., 2009 r:TCTTCTGGTACTAAAGTGG 384 Phuc Nguyen et al., 2009 r:GCCACTTATTGGGGGTAATGG 384 Phuc Nguyen et al., 2009 | | R:CTCGAATGCCTGGCGTGTTT | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| mphAF:GTGAGGAGGAGCTTCGCGAGG403Phuc Nguyen et al., 2009 R:TGCCGCAGGACTCGGAGGTCmphBF:GATATTAAACAAGTAATCAGAATAG494Phuc Nguyen et al., 2009 R:GCTCTTACTGCATCCATACGermAF:TCTAAAAAGCATGTAAAAGAAA533Phuc Nguyen et al., 2009 R:GCGTATCTTTTTGTAGTCCTTCermBF:GAAAAAGTACTCAACCAAATA693Phuc Nguyen et al., 2009 R:ATTTAAGTACCGTTACTereAF:GCCGGTGCTCATGAACTTGAG420Phuc Nguyen et al., 2009 R:CGACTCTATCGATCAGAGGCmefAF:AGTATCATTAATCACTAGTGC420Phuc Nguyen et al., 2009 R:CGACTCTATCGATCAGAGGGCmsrAF:GCACTTATTAGGGGGTAATGG345Phuc Nguyen et al., 2009 R:GTCTATAAGTGCGTTACTGTG | Macrolide-resistance Genes | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| R:TGCCGCAGGACTCGGAGGTC mphB F:GATATTAAACAAGTAATCAGAATAG 494 Phuc Nguyen et al., 2009 R:GCTCTTACTGCATCCATACG 8 Phuc Nguyen et al., 2009 ermA F:TCTAAAAAGCATGTAAAAGAAA 533 Phuc Nguyen et al., 2009 R:cGATACTTTTTGTAGTCCTTC 8 Phuc Nguyen et al., 2009 ermB F:GCAGATGCTCAACCAAATA 693 Phuc Nguyen et al., 2009 R:AATTTAAGTACCGTTACT 8 Phuc Nguyen et al., 2009 R:CGACTCATTCAACCAAATA 693 Phuc Nguyen et al., 2009 R:CGACTCATTCAGACCTAGGC 420 Phuc Nguyen et al., 2009 R:CGACTCTATTCGATCAGAGGC 10 10 10 mefA F:AGTATCATTAATCACTAGTGC 345 Phuc Nguyen et al., 2009 R:TTCTTCTGGTACTAAAAGTGG 10 10 10 msrA F:GCACTTATTGGGGGTAATGG 384 Phuc Nguyen et al., 2009 | mphA | F:GTGAGGAGGAGCTTCGCGAG | 403 | Phuc Nguyen et al., 2009 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| mphBF:GATATTAAACAAGTAATCAGAATAG494Phuc Nguyen et al., 2009R:GCTCTTACTGCATCCATACGF:TCTAAAAAGCATGTAAAAGAAA533Phuc Nguyen et al., 2009R:CGATACTTTTGTAGTCCTTCF:GAAAAAGTACTCAACCAAATA693Phuc Nguyen et al., 2009R:AATTTAAGTACCGTTACTF:GCCGGTGCTCATGAACCTGAGCPhuc Nguyen et al., 2009R:AATTTAAGTACCGTTACTF:GCCGGTGCTCATGAACTTGAGG420Phuc Nguyen et al., 2009R:CGACTCTATTCGATCAGAGGCF:GCCGGTGCTCATGAACTTGAG420Phuc Nguyen et al., 2009mefAF:AGTATCATTAATCACTAGTGC345Phuc Nguyen et al., 2009R:TCTTCTGGTACTAAAAGTGGImmodel alter alte | | R:TGCCGCAGGACTCGGAGGTC | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| R:GCTCTTACTGCATCCATACG ermA F:TCTAAAAAGCATGTAAAAGAAA 533 Phuc Nguyen et al., 2009 R:CGATACTTTTTGTAGTCCTTC ermB F:GAAAAAGTACTCAACCAAATA 693 Phuc Nguyen et al., 2009 R:AATTTAAGTACCGTTACT ereA F:GCCGGTGCTCATGAACCTAGAG 420 Phuc Nguyen et al., 2009 R:CGACTCTATTCGATCAGAGGC mefA F:AGTATCATTAACACTAGTGC 345 Phuc Nguyen et al., 2009 msrA F:GCACTTATTGGGGGTAATGG 384 Phuc Nguyen et al., 2009 | mphB | F:GATATTAAACAAGTAATCAGAATAG | 494 | Phuc Nguyen et al., 2009 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| emA F:TCTAAAAGCATGTAAAAGAAA 533 Phuc Nguyen et al., 2009 R:CGATACTTTTTGTAGTCCTTC emB F:GAAAAAGTACTCAACCAAATA 693 Phuc Nguyen et al., 2009 R:AATTTAAGTACCGTTACT ereA F:GCCGGTGCTCATGAACTTGAG 420 Phuc Nguyen et al., 2009 R:CGACTCTATTCGATCAGAGGC mefA F:AGTATCATTAATCACTAGTGC 345 Phuc Nguyen et al., 2009 R:TTCTTCTGGTACTAAAAGTGG msrA F:GCACTTATTGGGGGTAATGG 384 Phuc Nguyen et al., 2009 | , | R:GCTCTTACTGCATCCATACG | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
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| emB F:GAAAAGTACTCAACCAAATA 693 Phuc Nguyen et al., 2009 R:AATTTAAGTACCGTTACT ereA F:GCCGGTGCTCATGAACTTGAG 420 Phuc Nguyen et al., 2009 R:CGACTCTATTCGATCAGAGGC mefA F:AGTATCATTAATCACTAGTGC 345 Phuc Nguyen et al., 2009 R:TTCTTCTGGTACTAAAAGTGG msrA F:GCACTTATTGGGGGTAATGG 384 Phuc Nguyen et al., 2009 R:GTCTATAAGTGCTCTATCGTG | | R:CGATACTTTTTGTAGTCCTTC | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
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| ereA F:GCCGGTGCTCATGAACTTGAG 420 Phuc Nguyen et al., 2009 R:CGACTCTATTCGATCAGAGGC mefA F:AGTATCATTAATCACTAGTGC 345 Phuc Nguyen et al., 2009 R:TTCTTCTGGTACTAAAGTGGG msrA F:GCACTTATTGGGGGTAATGG 384 Phuc Nguyen et al., 2009 R:GTCTATAAGTGCTCTATCGTG | | R:AATTTAAGTACCGTTACT | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
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| mefA F:AGTATCATTAATCACTAGTGC 345 Phuc Nguyen et al., 2009 R:TTCTTCTGGTACTAAAAGTGG 384 Phuc Nguyen et al., 2009 msrA F:GCACTTATTGGGGGTAATGG 384 Phuc Nguyen et al., 2009 R:GTCTATAAGTGCTCTATCGTG 384 Phuc Nguyen et al., 2009 | | R:CGACTCTATTCGATCAGAGGC | - | 0.,, | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| msrA F:GCACTTATTGGGGGTAATGG R:GTCTTATAAGTGCTCTATCGTG 384 Phuc Nguyen et al., 2009 R:GTCTATAAGTGCTCTATCGTG | mefA | F:AGTATCATTAATCACTAGTGC | 345 | Phuc Nguven et al., 2009 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| msrA F:GCACTTATTGGGGGTAATGG 384 Phuc Nguyen et al., 2009 R:GTCTATAAGTGCTCTATCGTG | | R:TTCTTCTGGTACTAAAAGTGG | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| R:GTCTATAAGTGCTCTATCGTG | msrA | F:GCACTTATTGGGGGTAATGG | 384 | Phuc Nguven et al., 2009 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | R:GTCTATAAGTGCTCTATCGTG | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

isolates contained two types of antimicrobial-resistant genes: aac(6')-*Ib*-*cr*/*bla*_{TEM} (n = 2) and aac(6')-*Ib*-*cr*/*bla*_{CTX-M} (n = 2). In addition, 2 out of the 15 isolates that were

co-resistant to azithromycin concurrently harbored ESBL, PMQR, and *mphA* genes: *aac*(6')-*Ib-cr/bla*_{CTX-M}/*bla*_{TEM}/*mphA* (**Table 4**).



| TABLE 2 | Antimicrobial resistance of S. | Typhimurium isolates in | Shanghai from 2011 to 2014. |
|---------|--------------------------------|--------------------------|-----------------------------|
| | | Typinnianani loolatoo in | |

| | 2011 (<i>N</i> = 77) | 2012 (N = 155) | 2013 (N = 167) | 2014 (<i>N</i> = 160) | Total (N = 559) |
|-------------------------------|-----------------------|----------------|----------------|------------------------|-----------------|
| Pan-susceptible | 4 (5.2) | 8 (5.2) | 4 (2.4) | 10 (6.3) | 26 (4.7) |
| Nalidixic Acid | 67 (87) | 107 (60) | 145 (86.8) | 124 (77.5) | 443 (79.2) |
| Ciprofloxacin | 7 (9.1) | 4 (2.6) | 6 (3.6) | 3 (1.9) | 20 (3.6) |
| Ampicillin | 54 (70.1) | 124 (80) | 150 (89.8) | 120 (75) | 448 (80.1) |
| Ceftiofur | 23 (29.9) | 37 (23.9) | 30 (18) | 22 (13.8) | 112 (20) |
| Cefoxitin | 8 (10.4) | 17 (10.3) | 1 (0.6) | 2 (3.8) | 28 (5) |
| Ceftriaxone | 23 (29.9) | 37 (23.9) | 30 (18) | 22 (13.8) | 112 (20) |
| Tetracycline | 58 (75.3) | 124 (80) | 156 (93.4) | 130 (81.3) | 468 (83.7) |
| Streptomycin | 33 (42.9) | 74 (47.7) | 97 (58.1) | 96 (60) | 300 (53.7) |
| Gentamicin | 29 (37.7) | 62 (40) | 81 (48.5) | 35 (21.9) | 207 (37) |
| Chloramphenicol | 31 (40.3) | 86 (55.5) | 124 (74.3) | 66 (41.3) | 307 (54.9) |
| Azithromycin | 1 (1.3) | 13 (8.4) | 4 (2.4) | 13 (8.1) | 31 (5.5) |
| Sulfisoxazole | 27 (35.1) | 126 (81.3) | 156 (93.4) | 122 (76.3) | 431 (77.1) |
| trimethoprim/sulfamethoxazole | 31 (40.3) | 76 (49) | 97 (58.1) | 61 (38.1) | 265 (47.4) |
| amox-icillin/clavulanic acid | 9 (11.7) | 20 (12.9) | 5 (3) | 10 (6.3) | 44 (7.9) |
| MDR pattern | | | | | |
| \geq 3 antimicrobials | 56 (72.7) | 130 (83.9) | 159 (95.2) | 128 (80) | 473 (84.6) |
| \geq 4 antimicrobials | 51 (66.2) | 121 (78.1) | 147 (88) | 116 (72.5) | 435 (77.8) |
| \geq 5 antimicrobials | 40 (51.9) | 91 (58.7) | 125 (74.9) | 85 (53.1) | 341 (61) |
| \geq 6 antimicrobials | 25 (32.5) | 52 (33.5) | 91 (54.5) | 47(29.4) | 215 (38.5) |
| \geq 7 antimicrobials | 1 (1.3) | 0 (0) | 1 (0.6) | 4 (2.5) | 6 (1.1) |
| ACSSuT | 15 (19.5) | 42 (27.1) | 66 (39.5) | 38 (23.8) | 161 (28.8) |
| ACSSuT+CIP | 5 (6.5) | 6 (3.9) | 18 (10.8) | 11 (6.9) | 40 (7.2) |
| ACSSuT+CEP | 7 (9.1) | 15 (9.7) | 8 (4.8) | 6 (3.8) | 36 (6.4) |
| ACSSuT+AZI | 1 (1.3) | 2 (1.3) | 1 (0.6) | 6 (3.8) | 10 (1.8) |
| ACSSuT+CIP+CEP | 2 (2.6) | 0 (0) | 2 (1.2) | 2 (1.3) | 6 (1.1) |
| ACSSuT+CIP+CEP+AZI | 1 (0.2) | 0 (0) | 0 (0) | 0 (0) | 1 (0.2) |

CIP, Ciprofloxacin; CEP, cephalosporins; AZI, Azithromycin.



TABLE 3 | Distribution of PMQR genes and mutations in gyrA, gyrB, parC, and parE genes in S. Typhimurium isolates with decreased susceptibility to ciprofloxacin in Shanghai, China.

| | QRDR | mutation | PMQR | N | | Total | |
|-----------|------|-----------|------|--------------------|------------|-------|----|
| gyrA | gyrB | parC | parE | | I * | R** | |
| WT | WT | WT | WT | qnrS | 1 | 0 | 1 |
| WT | WT | WT | WT | aac(6')-lb-cr | 1 | 0 | 1 |
| WT | WT | WT | WT | aac(6')-lb-cr,qnrB | 1 | 3 | 4 |
| D87Y | WT | WT | WT | WT | 15 | 0 | 15 |
| D87Y | WT | WT | WT | aac(6')-lb-cr | 20 | 4 | 24 |
| D87N | WT | WT | WT | aac(6')-lb-cr | 13 | 4 | 17 |
| D87Y | WT | WT | WT | aac(6')-lb-cr,qnrB | 0 | 2 | 2 |
| S83F/D87N | WT | S80R | WT | WT | 0 | 4 | 4 |
| S83F/D87N | WT | S80R | WT | aac(6')-lb-cr | 0 | 1 | 1 |
| S83F/D87G | WT | S80R | WT | WT | 0 | 1 | 1 |
| S83F/D87N | WT | T57S/S80R | WT | aac(6')-lb-cr | 0 | 1 | 1 |

*S. Typhimurium isolates with intermediate resistance to CIP (MIC = 2 μ g/mL); **S. Typhimurium isolates with resistance to CIP (MIC \geq 4 μ g/mL); WT, wild type.

DISCUSSION

In present study, we found that *S*. Typhimurium isolates in Shanghai, China, exhibited high rates of resistance to traditional antimicrobials, such as tetracycline, ampicillin, nalidixic acid, and sulfisoxazole. Moreover, resistance to cephalosporins, ciprofloxacin and azithromycin were found in 20.6, 3.6, and 5.5% of the isolates, respectively. Contradictory to this result

from the current study, the report of the NARMS indicated that the number of cephalosporin-resistant, ciprofloxacin-resistant and azithromycin-resistant isolates was lower than 6, 1, and 1% (2011–2014), respectively (Centers for Disease Control and Prevention, 2016). More importantly, 84.6% of the isolates were found to exhibit MDR in our study, which is significantly higher than the percentage observed from the surveillance data during 2005 to 2010 in Shanghai and that indicated in

| Strain | | MIC (µg/mL) | | | | QRDR mutation | | PMQR | ESBL | mphA |
|------------|-----|-------------|-----|-----|-----|---------------|-----------|--------------------|---|------|
| | FOX | CRO | XNL | CIP | AZI | gyrA | parC | | | |
| SHI 1G663 | >32 | 4 | 8 | 4 | 4 | WT | WT | qnrB/aac(6')-lb-cr | | |
| SHI 1G664 | >32 | 8 | >8 | 4 | 2 | WT | WT | qnrB/aac(6')-lb-cr | bla _{OXA} | |
| SHI 1G665 | >32 | 32 | 8 | 4 | 4 | WT | WT | qnrB/aac(6')-lb-cr | bla _{OXA} | |
| SH11G680 | 4 | >64 | >8 | >4 | 2 | S83F/D87N | S80R | | bla _{OXA} /bla _{CTX-M-55} | |
| SHI 1G993 | >32 | 16 | >8 | >4 | 256 | S83F/D87N | S80R | | bla _{OXA} | mphA |
| SH11G1304 | 2 | >64 | >8 | 2 | 4 | D87Y | WT | aac(6')-lb-cr | bla _{OXA} /bla _{CTX-M-27} | |
| SH11G1306 | 2 | >64 | >8 | 2 | 4 | D87Y | WT | | | |
| SHI 2G734 | 32 | <0.25 | 2 | 2 | 4 | D87Y | WT | aac(6')-lb-cr | bla _{TEM} | |
| SHI 2G889 | 32 | <0.25 | 2 | 4 | 8 | D87Y | WT | aac(6')-lb-cr | bla _{OXA} /bla _{CTX-M-14} /bla _{TEM} | |
| SH12G978 | 32 | >64 | >8 | 2 | 64 | WT | WT | qnrB/aac(6')-lb-cr | bla _{CTX-M-15} /bla _{TEM} | |
| SHI 2G1005 | 8 | >64 | >8 | >4 | 64 | S83F/D87N | T57S/S80R | aac(6')-lb-cr | bla _{CTX-M-65} /bla _{TEM} | |
| SHI 3G355 | 2 | >64 | >8 | 2 | 4 | D87N | WT | aac(6')-lb-cr | bla _{TEM} | |
| SHI 3G769 | 2 | >64 | >8 | 2 | 4 | D87N | WT | aac(6')-lb-cr | bla _{CTX-M-14} | |
| SHI 3G938 | 16 | >64 | >8 | 2 | 4 | D87N | WT | | bla _{OXA} /bla _{CTX-M-55} | |
| SHI 3G939 | 16 | >64 | >8 | 2 | 4 | D87N | WT | | bla _{OXA} /bla _{CTX-M-55} | |
| SH13G1219 | 8 | >64 | >8 | >4 | 128 | D87Y | WT | aac(6')-lb-cr | bla _{CTX-M-15} /bla _{TEM} | mphA |
| SHI 3G1825 | 2 | >64 | >8 | >4 | 128 | D87Y | WT | aac(6')-lb-cr | bla _{CTX-M-15} /bla _{TEM} | mphA |
| SHI 4G287 | 4 | >64 | >8 | 2 | 8 | WT | WT | aac(6')-lb-cr | bla _{OXA} /bla _{CTX-M-125} | |
| SHI 4G294 | 8 | 64 | >8 | 2 | 8 | D87N | WT | aac(6')-lb-cr | bla _{OXA} /bla _{CTX-M-125} | |
| SHI 4G300 | 4 | 64 | >8 | 2 | 64 | D87N | WT | aac(6')-lb-cr | bla _{OXA} /bla _{CTX-M-125} | |
| SHI 4G1345 | 4 | >64 | >8 | 2 | 4 | D87Y | WT | | bla _{OXA} /bla _{CTX-M-55} /bla _{TEM} | |
| SH14G1601 | 2 | >64 | >8 | 2 | 4 | D87N | WT | aac(6')-lb-cr | bla _{CTX-M-55} | |

TABLE 4 | Summary of phenotypes of S. Typhimurium isolates showing concurrently decreased susceptibility to ciprofloxacin and cephalosporins and their corresponding resistance genes.

FOX, cefoxitin; CRO, ceftriaxone; XNL, ceftiofur; CIP, ciprofloxacin; AZI, azithromycin; WT, wild type.

the NARMS report for the same period (P < 0.05) (Zhang et al., 2014; Centers for Disease Control and Prevention, 2016). Notably, in the current study, we found that 22 MDR isolates with decreased susceptibility to ciprofloxacin were coresistant to cephalosporins. Six of the 22 isolates also showed resistance to azithromycin. This phenomenon has only been reported previously in two clinical S. Typhimurium strains in China (Wong et al., 2014). If these MDR strains are as prevalent as S. Typhimurium DT104 all over the world, it will pose a great threat to global public health. Our findings indicate that it is therefore necessary to continue monitoring the antimicrobial resistance of S. Typhimurium isolates to help determine the appropriate antimicrobial therapy for patients with S. Typhimurium infection. More importantly, it is necessary to study the mechanisms underlying the antimicrobial resistance in these isolates.

The main mechanisms of quinolone-resistance in *Salmonella* have been attributed to several point mutations in the QRDRs of the *gyrA* and *parC* genes and the PMQR genes (Hopkins et al., 2007; Kim et al., 2013). Mutations at different sites contribute to different levels of resistance to ciprofloxacin, and simultaneous mutations in both *gyrA* and *parC* genes produce high levels of ciprofloxacin resistance. Besides, most isolates with decreased susceptibility to ciprofloxacin contain a mutation in *gyrA* or PMQR genes (Ling et al., 2003; Lin et al., 2015). In the present study, we found that six isolates had double mutations (S83F/D87N or D87G) in the *gyrA* gene and a single

mutation (S80R) in the parC gene. Additionally, one isolate with four mutations, including two in gyrA gene (S83F/D87N) and two in parC gene (T57S/S80R). These mutations have been previously reported to be most common in ciprofloxacinresistant S. Typhimurium strains (Wasyl et al., 2014). PMQR was initially identified in Klebsiella pneumonia in 1998 (Martinez-Martinez et al., 1998), since then, various types of PMQR genes have been detected in Salmonella all over the world (Cattoir et al., 2007; Cavaco et al., 2009; Kim et al., 2013). Previous studies have shown that the presence of qnr genes increase the MICs for ciprofloxacin by 8-16-fold (Kim et al., 2013). In addition, the presence of aac(6')-Ib-cr genes can increase the selection of chromosomal mutants that cause ciprofloxacin resistance (Robicsek et al., 2006). In the current study, we also showed that the existence of PMQR genes remarkably enhances the MICs $(\geq 2 \ \mu g/mL)$ of ciprofloxacin in the presence of a single or no point mutation in the gyrA gene in S. Typhimurium isolates. The emergence of PMQR genes described in this report has also been frequently reported previously in Salmonella isolates in other parts of China (Lu et al., 2011; Jiang et al., 2014; Wong et al., 2014), which suggests that the PMQR genes have been prevalent in China.

Since the discovery of $bla_{\text{CTX-M}}$ genes in Japan, Europe, and South America in the 1980s (Matsumoto et al., 1988; Bauernfeind et al., 1990, 1992), they have quickly replaced bla_{TEM} and bla_{SHV} as the major ESBL (D'Andrea et al., 2013). In the present study, of the 115 cephalosporin-resistant isolates, 62.5% harbored $bla_{\text{CTX-M}}$ genes, in which $bla_{\text{CTX-M-55}}$ was the most common gene, followed by $bla_{\text{CTX-M-14}}$. This phenomenon proved that the $bla_{\text{CTX-M-1}}$ and $bla_{\text{CTX-M-9}}$ groups are popular types in *S*. Typhimurium isolates in Shanghai. Besides, the subtypes of $bla_{\text{CTX-M-123}}$ and $bla_{\text{CTX-M-125}}$ have also been identified in *E. coli* (Rao et al., 2014), but have not been found in *Salmonella*. To the best of our knowledge, this study is the first to report $bla_{\text{CTX-M-123}}$ and $bla_{\text{CTX-M-125}}$ in *S*. Typhimurium. In addition, 52 (45.2%), 43 (37.4%), and 3 (2.6%) isolates were found to contain the $bla_{\text{TEM-1}}$, $bla_{\text{OXA-1}}$, and $bla_{\text{SHV-12}}$ genes, respectively. Because the ESBL genes are usually located on the antimicrobial-resistance plasmid of the bacteria, they can be easily disseminated between different species of bacteria with the transfer of the drug-resistance plasmid (Arlet et al., 2006).

As the number of cephalosporin-resistant and ciprofloxacinresistant Salmonella strains gradually increased, an alternative antimicrobial class was needed to manage Salmonella infections. Azithromycin showed excellent ability to accumulating at high intracellular concentrations, and it achieved intracellular concentrations of 50 to 100 times greater than the serum levels (Panteix et al., 1993). Therefore, azithromycin was recommended for the treatment of invasive Salmonella infections by the FAD (Sjolund-Karlsson et al., 2011). However, in the present study, 31(5.5%) isolates were found to be resistant to azithromycin. Previously, Salmonella strains resistant to azithromycin have also been found in other countries (Sjolund-Karlsson et al., 2011; Kalonji et al., 2015). The plasmidborne mphA gene was reported as one of the reasons of azithromycin-resistance (Glynn et al., 1998). In the present study as well, 15 high-level azithromycin-resistant isolates (MIC > 128 μ g/mL) harbored the *mphA* gene, while other 16 (MIC: 16-64 µg/mL) did not. All azithromycin-resistant isolates were negative for mphB, ermA, ermB, ereA, mefA, and msrA. These results indicate that the mphA gene may mediate a high level of resistance to azithromycin in Salmonella, as described previously in Shigella in China (Zhang et al., 2016). In addition, azithromycin resistance may arise from other possible mechanisms, such as mutations in the rlpD and rlpV genes (Roberts, 2008). At present, few studies have been focused on investigating azithromycin resistance mechanisms in Salmonella. The findings of the present study and those of other previous studies emphasize the need for investigating the further mechanisms underlying azithromycin resistance in Salmonella isolates.

Antimicrobial-resistance genes are usually located on plasmids and therefore can be easily disseminated; for example

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the ESBL genes often coexist with the genes encoding resistance to other antimicrobial agents in plasmids, which can easily lead to a MDR phenotype in ESBL-producing bacteria (Jiang et al., 2014). In this study, we found that 15 isolates showed both ESBL and PMQR genes, in which concurrently displayed decreased susceptibility to cephalosporins and ciprofloxacin. Besides, 2 of the 15 isolates co-contained *mphA* genes, which were resistant to azithromycin.

CONCLUSION

In this study, we reported the common occurrence of MDR in *S*. Typhimurium isolates in Shanghai, China. We found that resistance to ciprofloxacin, cephalosporins, and azithromycin was most prevalent among the isolates. Among the MDR isolates, we found various transferrable antimicrobial-resistance genes, which included ESBL, PMQR and *mphA* genes, and some isolates even contained at least two types of these genes. The dissemination of these genes poses a huge threat to the control of *S*. Typhimurium infection in the world. Our findings indicate that it is imperative to continue monitoring the prevalence of the above-mentioned three types of antimicrobial resistance and their resistant genes in *S*. Typhimurium isolates. Future studies should be focused on identifying ways to prevent the dissemination of these antimicrobial-resistance genes.

AUTHOR CONTRIBUTIONS

SQ, HS, and JW designed the study, XX participated in the collection of the samples. BL, FW, XY, CS, XH, and JX completed identification and preservation of samples, YL, XD, HaL, and JW were responsible for the experiments. JW, QM, HoL, RH, and CY analyzed the data. JW wrote the manuscript, and SQ and HS provided academic revision for the manuscript. All the authors have read and approved the final draft of the manuscript.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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