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Genetic characterization and in silico serotyping of 62 *Salmonella enterica* isolated from Korean poultry operations

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Abstract

Background The conventional method of antigen-based serotyping for *Salmonella* poses challenges due to the necessity of utilizing over 150 antisera. More recently, in silico *Salmonella* serotyping has emerged as a predictive alternative. The purpose of this study was to predict the serovars of 62 *Salmonella enterica* strains isolated from Korean poultry operations and their genetic characteristics using whole genome sequencing. The analysis employed diverse methods, including ribosomal, and core genome multi-locus sequence typing (MLST), based on *Salmonella* In Silico Typing Resource (SISTR). Pangenome, clusters of orthologous groups (COG) analysis, and identification of virulence and antibiotic resistance genes were conducted.

Results *Salmonella enterica* subspecies *enterica* serovars were observed and clustered based on the pangenome and phylogenetic tree: 21 *Salmonella* Albany (Albany), 13 *Salmonella* Bareilly (Bareilly), and 28 *Salmonella* Mbandaka (Mbandaka). The most frequently observed sequence types for the three serovars were ST292 in Albany, ST203 in Bareilly, and ST413 in Mbandaka. 18 antibiotic resistance genes showed varying presences based on the serovars, including Albany (*qacEdelta1*, *tet(D)*, CARB-3 (*blaCARB-3*), and *dfrA1*) and Bareilly (*aac(6')-ly*). Intriguingly, a mutated *gyrA* (Ser83 → Phe, serine to phenylalanine) was observed in all 21 Albany strains, whereas Bareilly and Mbandaka carried the wild-type *gyrA*. Among 130 virulence genes analyzed, 107 were present in all 62 *Salmonella* strains, with Mbandaka strains exhibiting a higher prevalence of virulence genes related to fimbrial adherence compared to those of Albany and Bareilly.

Conclusions The study identified distinct genetic characteristics among the three *Salmonella* serovars using whole genome sequencing. Albany carried a unique mutation in *gyrA*, occurring in the quinolone resistance-determining region. Additionally, the virulence gene profile of Mbandaka differed from the other serovars, particularly in fimbrial adherence genes. These findings demonstrate the effectiveness of in silico approaches in predicting *Salmonella* serovars and highlight genetic differences that may inform strategies for antibiotic resistance and virulence control, such as developing rapid diagnostic tools to detect the AMR (e.g. *tet (D),* and *gyrA*) or targeting serovar-specific virulence factors like fimbrial adherence genes in Mbandaka to mitigate pathogenicity.

Keywords *Salmonella enterica*, In silico serotyping, Whole genome sequencing, *gyrA* mutant

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Background

Salmonella species are ubiquitous foodborne pathogens associated with a variety of food sources, including fresh produce, eggs, peanut butter, poultry, and meat [1]. The Centers for Disease Control and Prevention (CDC) reports that *Salmonella* infection results in 1.35 million cases of salmonellosis, 26,500 hospitalizations, and 420 deaths in the United States annually [2]. *Salmonella enterica* isolates usually cause salmonellosis in humans and animals usually causes diarrhea, fever, and stomach cramps [2], and sometimes results in more invasive illness infecting the blood, bones, or nervous system. The United States Department of Agriculture (USDA) have reported that salmonellosis is one of the most frequently reported foodborne illness caused by bacteria [3].

Salmonella enterica subsp. *enterica* serovars, notably Bareilly, have been implicated in numerous outbreaks of foodborne illness, often associated with raw or undercooked seafood products like tuna. For example, in 2012, a multistate outbreak in the US was linked to contaminated frozen raw yellowfin tuna product ("tuna scrape"), which sickened 425 people across 28 states [4–6]. Bareilly, associated with paratyphoid fever, was first reported in a fish facility in India in 1928 and has since been steadily reported in countries like the UK and the US [7]. Meanwhile, salmonellosis has been consistently reported in Asian countries, contributing to approximately 7.7% of foodborne illnesses in South Korea [8–10]. Serovars such as Albany, Enteritidis, and Montevideo have been frequently isolated from poultry facilities in South Korea [11, 12]. In 2019, an outbreak associated with Thompson occurred in 10 schools in Busan, South Korea. This outbreak was related to a chocolate cake served in the school lunch program. In total, the outbreak sickened 207 individuals, with 92 (44.4%) of the cases linked to consuming the chocolate cake [13]. Furthermore, studies in South Korea have identified commonly reported serovars associated with human infections in South Korea, including Enteritidis, Typhimurium (1998–2007), and Bareilly (2016–2017) [14, 15]. However, the specific serovars originating from primary food sources such as chicken remain inadequately understood. To address this knowledge gap, it is imperative to utilize up-to-date and molecular serotyping methods while gaining a comprehensive understanding of their genetic characteristics.

Identifying the vast diversity of *Salmonella* serovars typically involves agglutination with specific antisera to distinguish somatic (O) and flagella (H) antigens, a time-consuming process requiring over 150 antisera [16]. Traditional methods, including phenotypic typing, phage typing, and PCR, have been used for decades but are prone to errors and labor-intensive [1, 17, 18]. To address these limitations, modern approaches like whole genome sequencing (WGS) have emerged as powerful tools for comprehensive genomic characterization of *Salmonella*.

WGS is a powerful technique employed to identify the complete DNA sequence of an organism's genome, facilitating a comprehensive analysis of its genetic material [19, 20]. This method has been increasingly adopted for characterizing and tracing foodborne pathogens, enabling rapid detection of variants and identification of causative factors for illnesses as an alternative to pulsed-field gel electrophoresis (PFGE) [19–21]. For instance, in the general bioinformatics assays that focus on performing WGS onto pathogenic bacterial DNA, analyzable results could be obtained within 14–22 h of sequencing, significantly reducing the overall sequencing-to-results time and enabling faster response in outbreak investigations [21]. In addition, WGS data can be applicable to examine genetic characteristics including virulence, resistance genes, and biological attributes of genomes using multi-locus sequence typing (MLST) and other genomic parameters in the food safety field. In silico serotyping based on WGS is also available for the characterization of *Salmonella* using bioinformatic programs and software [22]. Virulence genes, whose products can increase the severity of illness, are typically found in *Salmonella* including *Salmonella* pathogenicity islands (SPIs) and mobile genetic elements (MGEs) such as plasmids. The presence of these elements varies depending on serovar-specific genes. Antibiotic resistance genes in the pathogen can resist drugs designed to eliminate pathogen, survive exposure to antimicrobials, and continue multiplying in the human body. Antibiotic resistance genes have been steadily reported to contribute to salmonellosis in humans and animals [23]. Based on the antimicrobial resistance genes, pathogenicity can be also determined [24]. Therefore, identifying serovar, virulence factors, and antibiotic resistance genes is important in order to characterize *Salmonella*.

Given the transformative capabilities of WGS, the aim of this study to leverage the transformative advancements in WGS to characterize and type a collection of *Salmonella* strains isolated from Korean poultry operations. More specifically, the objectives were to identify the serovars of 62 *Salmonella* using MLST and pangenome for their clustering based on the WGS. In addition, we sought to analyze the genetic characteristics of each group, focusing on virulence factors and antibiotic resistance genes.

Methods

Salmonella strains

The 62 *Salmonella enterica* strains analyzed in this study were obtained from poultry feces collected by our collaborator from 18 poultry farms (2 in the capital region,

4 in the Chungcheong region, 5 in the Gangwon region, 3 in the Southwestern region, and 4 in the southeastern region) and 10 slaughterhouses (3 in the capital region, 1 in the Chungcheong region, 2 in the Gangwon region, 3 in the Southwestern region, and 1 in the Southeastern region) across Korea in 2018 [25]. The samples from slaughterhouses were taken during six processing stages: suspension, before/after de-feathering, rinsing, evisceration, and chilling. Briefly, xylose-lysine-deoxycholate agar (XLD, Becton, Dickinson and Company, Sparks, MD) was used to differentiate *Salmonella* species [25]. Genomic DNA was extracted using a Qiagen DNeasy Blood and Tissue kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. The concentration of extracted DNA was measured using a Qubit 4 Fluorometer (Thermo Fisher Scientific, Waltham, MA, USA) and diluted to 10 ng/ul for WGS analysis.

Library preparation and sequencing

The pooled library for WGS was generated using a Nextera XT Library Prep Kit (Illumina, San Diego, CA, USA) according to the manufacturer's procedure. Briefly, the segmentation step was performed to fragment DNA, and indexed fragments were amplified using a thermocycler (Eppendorf Master cycler, Nexus Gradient, Germany). The library was meticulously cleaned using Illumina purification beads and an 80% ethanol solution. Following this, the normalization step was executed to guarantee a well-balanced library, using Library Normalization beads 1 and 2 provided by the manufacturer and 0.1 N NaOH. Finally, the library was diluted to the proper concentration and sequenced using an Illumina MiSeq system (2 × 250 bp, 500 cycles) in the Center for Quantitative Life Sciences at Oregon State University.

Genome assembly, annotation, and in silico genotyping

Short reads from 62 *Salmonella* strains were assembled using the QAssembly pipeline in EnteroBase v1.2.0 [26]. The QAssembly pipeline is a comprehensive pipeline that includes trimming of raw reads, genome assembly, and evaluation of assembled genome. The programs used for each step in this pipeline are as follows. First, raw reads were trimmed using Sickle v1.33 [27] with a quality score threshold of 10. Next, draft genome assembly was performed using SPAdes v3.9.0 [28]. BWA v0.7.18, SAMtools v1.20, and BCFtools v 1.20 [29, 30] were used for remapping and consensus base calling to generate the assemblies. Finally, the assembled genomes were evaluated by the criteria for *Salmonella* strains: number of bases 4—5.8 Mbp, N50 value > 20 kb, number of contigs < 600, proportion of scaffolding placeholders (N's) < 3%, and species assignment based on a modified Kraken alignment (assigned contigs > 70%) [31–33]. The 62 strains were subjected to gene annotation and in silico serotyping analyses in the Enterobase pipeline [26]. Structural and functional gene annotation were performed using Prokka v1.14.5 [34]. In silico genotyping was performed for serotyping and three MLST methods: seven gene MLSTs, ribosomal MLST (rMLST), and core genome MLST (cgMLST). The seven housekeeping genes included *aroC, dnaN, hemD, hisD*, *purE*, *sucA*, and *thrA*. The cgMLST was analyzed using EnteroBase with 3,002 target loci. No additional hierarchical clustering (HC) thresholds were applied; HC0, which groups isolates based on exact matches of allelic profiles across all loci, was used for the highest resolution.

Pangenome and functional enrichment analysis

The pangenome of 62 *Salmonella* isolates was generated using a modified version of method described in the previous study [35]. According to the Anvi'o pangenome pipeline v6.0, phylogenetic analysis of 62 *Salmonella* genomes was executed [36]. The 'anvi-gen-genomes-storage' program in the Anvi'o pipeline was used to create genome storage databases that contain data about explored genomes, which could then be used for phylogenetic analysis. Through the 'anvi-pan-genome' program, the produced genome storage was submitted to pangenomic analysis with default settings. Next, the pangenome was generated based on gene cluster frequencies and shown using an 'anvi-display-pan' program. This pangenome displayed the core and accessory gene clusters. Core gene clusters were defined as those present in all genomes, while accessory gene clusters were defined as all other gene clusters excluding core gene clusters. The average nucleotide identity (ANI) was calculated using a pyANI program v0.2.13.1 [37], and the values were represented by a heatmap. Different serovars were compared for their gene functionality using an 'anvi-compute-functional-enrichment-across-genomes' program, with the annotation source option set to 'COG20-CATEGORY' and adjusted q-value ($q < 0.05$). Then, enriched functions categorized by COGs in each serovar or in two serovars were analyzed with Anvi'o's enrichment scores with the adjusted q-value ($q < 0.05$), and COG categories were assigned in 62 *Salmonella* strains. It is important to note that a single function may correspond to one or more COG categories, and these were separated and calculated individually to ensure accuracy.

Prediction of antibiotic resistance and virulence factor genes

Antibiotic resistance and virulence genes were analyzed as previously described [38]. For the genes in 62 *Salmonella* strains, antimicrobial resistance (AMR) genes were predicted using the Resistance Gene Identifier

(RGI) v6.0.1 in the Comprehensive Antibiotic Resistance Database (CARD) v3.1.1 [39]. The 62 assembled FASTA files were used as the inputs. The antibiotic resistance genes were identified using the following options: DNA sequence, perfect and strict hits only, exclude nudge, and high quality/coverage. Virulence factor genes of 62 *Salmonella* isolates were predicted using the VF analyzer in the Virulence Factors Database (VFDB) v2022 [40] through the BV-BRC platform [41], which uses BLASTp with a sequence identity threshold of 80% and a coverage threshold of 70%.

Results

In silico genotyping analysis of 62 *Salmonella* strains

The serovar of 62 *Salmonella* strains was identified using in silico genotyping method, resulting in 21 strains of Albany, 13 of Bareilly, and 28 of Mbandaka strains (Table 1). Subsequent in silico multi-locus sequence typing (MLST) analyses were performed on these strains. The classical and ribosomal MLST methods, utilizing seven housekeeping genes and 53 genes encoding ribosomal proteins, respectively, identified specific sequence types (ST) and ribosomal sequence types (rST) for each serovar. All 21 Albany strains were associated with ST292 and rST7869, while all 13 Bareilly strains were assigned to ST203 and rST3715. Among the 28 Mbandaka strains, the majority of strains were classified as ST413 (27 strains) and rST3668 (27 strains). For one strain, rST was not determined, however, it was identified as Mbandaka. The strain with the undetermined rST shared seven alleles (*dnaN, hisD, purE, sucA, thrA, aroC*, and *hemD*) with ST413. However, while the *aroC* gene was present in the strain, its allele could not be assigned to the rST because it represents a novel sequence not cataloged in the MLST database. Similarly, a previous study reported variants at *aroC* locus in Typhimurium [42]. Another strain was assigned to ST10378 and rST3668, and it also belonged to Mbandaka. Interestingly, the allele profiles of ST10378 and ST413 differed in only one gene, *hisD*. The core genome sequence type (cgST), based on the set of conserved core genes that exist throughout the *Salmonella* genus, showed high resolution and revealed genomic variability among the 62 strains. Specifically, 28 Mbandaka strains were classified into 27 distinct cgSTs, while the 13 Bareilly and 21 Albany strains were categorized into 12 and 21 cgMLSTs, respectively.

Pangenome and COG analysis

The pangenome analysis of 62 *Salmonella* genomes identified a total of 5,415 gene clusters (Fig. 1A). Among these clusters, 3,743 were identified as core gene clusters, while 1,672 were classified as accessory gene clusters, indicating variability among the strains in this study. Each serovar exhibited a distinct pattern of gene cluster presence and absence in the pangenome. Although the ANI was very high (over 98%) because all strains were one species, *Salmonella enterica*, the heatmap revealed distinct genetic relatedness between the strains of each serovar.

To investigate gene functionality among the 62 strains, all gene clusters were annotated to the COG functional categories. Overall, the number of COGs was higher in the core gene clusters, with the exception of the X category, describing mobilome elements such as prophages and transposons. The functional enrichment analysis was conducted using annotated gene clusters to identify significantly enriched functions in specific serovars, the result of which is depicted in Fig. 1B (adjusted q-value < 0.05). Albany exhibited higher enrichment in the M category (cell wall/membrane/envelope biogenesis), while Albany and Mbandaka demonstrated significantly higher numbers in the X category (mobilome: prophages and transposons). Albany and Bareilly were highly enriched in the V category (defense mechanisms).

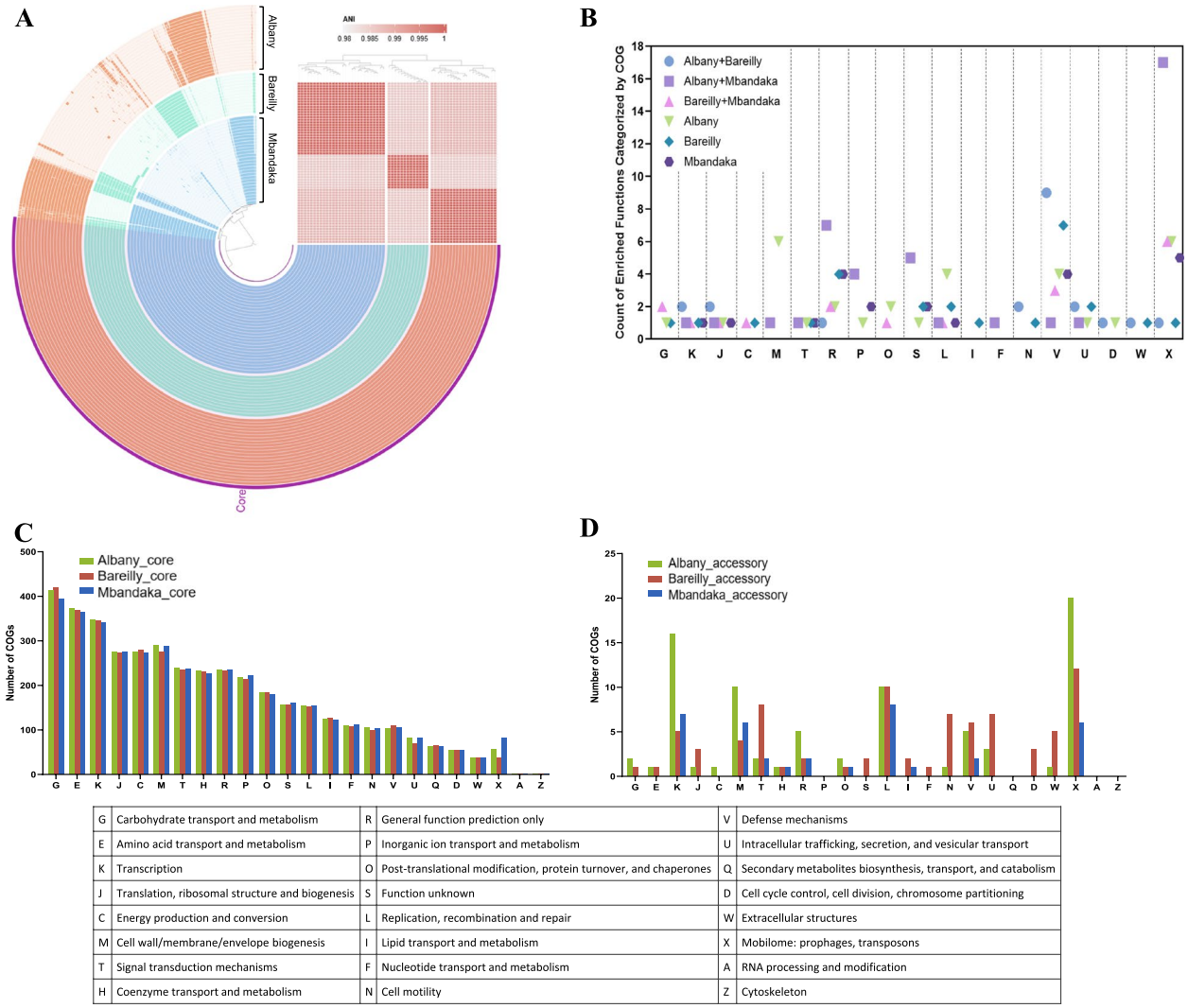
Furthermore, pangenomes of each serovar were compared with respect to the number of COGs (Fig. 1C-D). Pangenome analyses revealed that 21 Albany strains

Table 1 Results of different in silico typing for 62 *Salmonella enterica* strains

Serovar (SISTR)	MLST	rMLST	cgMLST
Albany (21)	ST292 (21)	rST7869 (21)	cgST350361, 350,370, 350,460, 350,377, 350,360, 350,364, 350,359, 350,458, 350,459, 350,466, 350,467, 350,468, 350,717, 350,723, 350,375, 350,725, 350,727, 350,729, 350,732, 350,755, 350,832
Bareilly (13)	ST203 (13)	rST3715 (13)	cgST350367, 350,368, 350,374 (2), 350,378, 350,461, 350,464, 350,465, 350,710, 350,713, 350,730, 350,831, 350,738
Mbandaka (28)	ST413 (27) ST10378 (1)	rST3668 (27) ND[a] (1)	cgST350369, 350,363, 350,358, 350,376, 350,365 (2), 350,379, 350,380, 350,362, 350,462, 350,711, 350,712, 350,714, 350,715, 350,716, 350,718, 350,719, 350,720, 350,721, 350,722, 350,724, 350,726, 350,728, 350,731, 350,733, 350,735, 350,830, 350,739

62 *Salmonella enterica* subsp. *enterica* were analyzed: 21 *Salmonella* Albany (Albany), 13 *Salmonella* Bareilly (Bareilly), and 28 *Salmonella* Mbandaka (Mbandaka). Serotyping and multilocus sequence typing (seven gene MLST, rMLST, and cgMLST) were performed using the Enterobase pipeline. The results were represented by the serovar or sequence type (the number of strains assigned)

[a] *ND* not determined



G	Carbohydrate transport and metabolism	R	General function prediction only	V	Defense mechanisms
E	Amino acid transport and metabolism	P	Inorganic ion transport and metabolism	U	Intracellular trafficking, secretion, and vesicular transport
K	Transcription	O	Post-translational modification, protein turnover, and chaperones	Q	Secondary metabolites biosynthesis, transport, and catabolism
J	Translation, ribosomal structure and biogenesis	S	Function unknown	D	Cell cycle control, cell division, chromosome partitioning
C	Energy production and conversion	L	Replication, recombination and repair	W	Extracellular structures
M	Cell wall/membrane/envelope biogenesis	I	Lipid transport and metabolism	X	Mobilome: prophages, transposons
T	Signal transduction mechanisms	F	Nucleotide transport and metabolism	A	RNA processing and modification
H	Coenzyme transport and metabolism	N	Cell motility	Z	Cytoskeleton

Fig. 1 Pangenome and functional enrichment analysis conducted on 62 *Salmonella enterica* isolates from Korean poultry operations. **A** Pangenome of 62 *Salmonella enterica* genomes (Albany, Bareilly, and Mbandaka). The average nucleotide identity (ANI) was represented by the heatmap, and the dendrogram on the top of the ANI heatmap was generated by the presence and absence of gene clusters. **B** Count of enriched functions categories by COGs (Clusters of Orthologous Groups) in different serovars. **C** The number of COG categories assigned to core gene clusters of each serovar. **D** The number of COG categories assigned to accessory gene clusters of each serovar

exhibited 4,143 core and 359 accessory gene clusters. Similarly, Bareilly ($n=13$) and Mbandaka ($n=28$) possessed 4,135 and 4,203 core gene clusters, along with 330 and 284 accessory gene clusters, respectively. The abundance of accessory gene clusters was lower than that in the 62 strains' genomes, suggesting that strains from the same serovar share similar genomic characteristics and reinforcing homogeneity within these serovars. Accessory genes of Albany were highly enriched in mobile genetic elements and genes associated with transcription. All gene clusters and their corresponding functional annotations, as generated by the pangenome analyses, are described in a supplementary Table 1 (Table S1).

Prevalence of virulence and antimicrobial resistance genes

The virulence and antibiotic resistance genes were predicted and explored in relation to the different serovars (Fig. 2). A total of 132 virulence factor genes were detected, 109 of which were found across all 62 strains. The presence/absence patterns of the remaining 23 variable virulence genes were used to describe Fig. 2, resulting in the identification of varying numbers of profiles: five in Albany, three in Bareilly, and seven in Mbandaka (profile information available in the supplementary table S2 and S3). Notably, strains of Mbandaka exhibited a higher prevalence of genes associated with fimbrial adherence (*faeC/D/E/* and *lpfA/B/C/E*) than strains of the other two

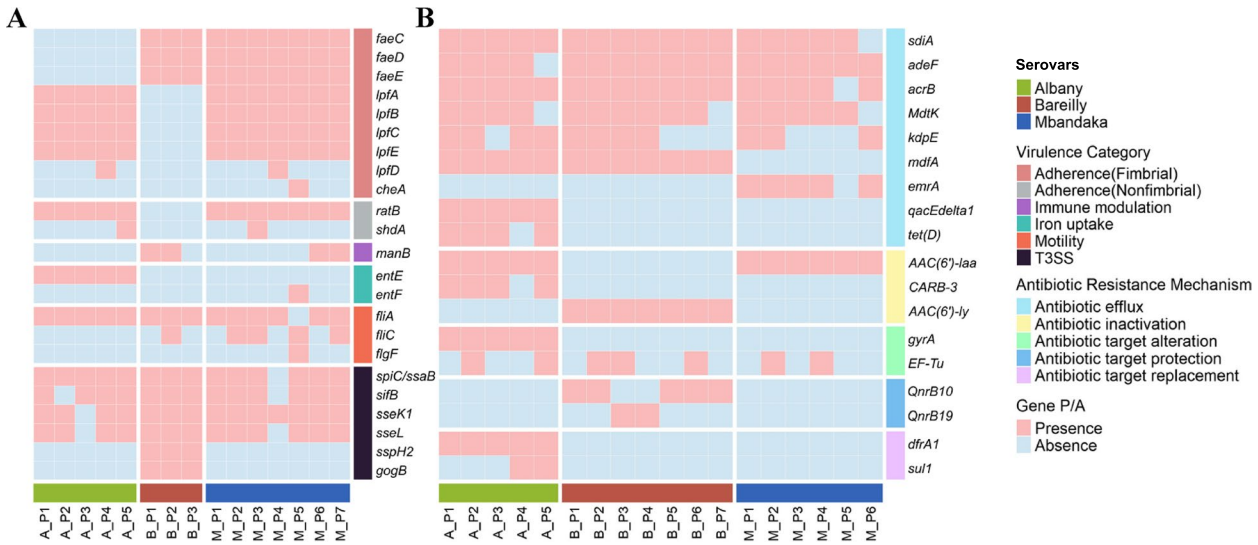


Fig. 2 Prediction of genes associated with virulence and antibiotic resistance of 62 *Salmonella enterica* strains; **A** Virulence genes, **B** Antibiotic resistance genes. The x-axis denotes (serovar abbreviation) (profile number). Isolates sharing identical gene presence and absence profiles within each *Salmonella enterica* serovar (Albany, A; Bareilly, B; Mbandaka, M) were clustered together based on patterns (P). T3SS: type III secretion system. All predicted genes associated with virulence and antibiotic resistance are detailed in Table S2-3

serovars. The *sspH2* and *gogB* genes, categorized into the type III secretion system (T3SS), were uniquely identified within the serovar Bareilly (Fig. 2A, Table 2). The comprehensive analysis on virulence genes of 62 *Salmonella* strains is available in Table S2.

A total of 41 antibiotic resistance genes were predicted, 18 of which were analyzed in association with the three serovars, excluding 23 genes present in the 62 *Salmonella* strains (Fig. 2B, Table 3). Overall, the 62 *Salmonella* strains contained more than three antibiotic resistance genes in their WGS data, indicating multidrug-resistant strains (e.g., fluoroquinolones, glycopeptides, aminoglycosides, and tetracyclines). Similar to the pathogenicity results, some genes were identified as specific features of the particular serovars. Genes classified as antibiotic efflux mechanisms were broadly identified in all three serovars, although *qacEdelta1* and *tet*(D) genes were exclusive to strain of serovar Albany, and a gene *emrA* was exclusive to strains of serovars Mbandaka. Albany exhibited five unique genes (*qacEdelta1, tet*(D), CARB-3 (*blaCARB-3*), *gyrA,* and *dfrA1*) representing four different antibiotic mechanisms, indicating a higher potential

Table 2 Prevalence of virulence genes in 62 *Salmonella enterica* serovars

Virulence category	Gene	Product	Serovar (No. of strains)
Adherence (Fimbrial)	*faeC*	K88 fimbrial protein FaeC	Bareilly (13), Mbandaka (28)
	faeD	K88 fimbrial usher FaeD	Bareilly (13), Mbandaka (28)
	faeE	K88 fimbrial chaperone FaeE	Bareilly (13), Mbandaka (28)
	lpfA	Long polar fimbria protein A	Albany (21), Mbandaka (28)
	lpfB	Chaperone protein LpfB	Albany (21), Mbandaka (28)
	lpfC	Outer membrane usher protein LpfC	Albany (21), Mbandaka (28)
	lpfE	Long polar fimbrial protein LpfE	Albany (21), Mbandaka (28)
Adherence (Nonfimbrial)	*ratB*	Putative outer membrane protein	Albany (21), Mbandaka (28)
Iron uptake	*entE*	(2,3-dihydroxybenzoyl) adenylate synthase EntE	Albany (21)
Type III secretion system (T3SS)	*sspH2*	Type III secretion system effector E3 ubiquitin transferase SspH2	Bareilly (13)
	gogB	Type III secretion system effector GogB	Bareilly (13)

62 *Salmonella enterica* subsp. *enterica* were analyzed: 21 *Salmonella* Albany (Albany), 13 *Salmonella* Bareilly (Bareilly), and 28 *Salmonella* Mbandaka (Mbandaka). A total of 130 genes were predicted and 107 genes among 130 genes were present in all of 62 strains in this study. Eleven genes present in specific serovar were shown in this table. The entire information of virulence genes is available in the Table S2

Table 3 Prevalence of antibiotic resistance genes in specific *Salmonella enterica* serovars

Antibiotic mechanism	Gene name	AMR gene family	Drug class	Serovar (No. of strains)
Antibiotic efflux	*mdfA*	Major facilitator superfamily (MFS) antibiotic efflux pump	Disinfecting agents and antiseptics, Tetracycline antibiotic	Albany (21), Bareilly (13)
	emrA		Fluoroquinolone antibiotic	Mbandaka (28)
	qacEdelta1		Disinfecting agents and antiseptics	Albany (21)
	tet(D)		Tetracycline antibiotic	Albany (21)
Antibiotic inactivation	*aac(6')-ly*	AAC(6')	Aminoglycoside antibiotic	Bareilly (13)
	bla_{CARB-3}	CARB beta-lactamase	Penam (Penicillin antibiotic)	Albany (21)
Antibiotic target alteration	*gyrA*	Fluoroquinolone resistant *gyrA*	Fluoroquinolone antibiotic	Albany (21)
Antibiotic target protection	*qnrB10*	Quinolone resistance protein (qnr)	Fluoroquinolone antibiotic	Bareilly (13)
Antibiotic target replacement	*dfrA1*	Trimethoprim resistant dihydrofolate reductase (dfr)	Diaminopyrimidine antibiotic	Albany (21)

62 *Salmonella enterica* subsp. *enterica* were analyzed: 21 *Salmonella* Albany (Albany), 13 *Salmonella* Bareilly (Bareilly), and 28 *Salmonella* Mbandaka (Mbandaka). A total of 41 genes were predicted and 23 genes among 41 genes were present in 62 strains in this study. Nine genes preset in specific serovar were shown in this table. The entire information of antibiotic resistance genes is available in the Table S3

threat to public health posed by Albany strains. In addition, only strains of serovar Bareilly carried *aac(6')-ly* (antibiotic inactivation), which encodes aminoglycoside resistance. Detailed antibiotic resistance genes of 62 *Salmonella* strains is available in the Table S3.

Quinolone resistance-determining regions (QRDRs) of *gyrA*

As a result of gene annotation using Prokka, *gyrA,* one of the essential genes encoding gyrase subunit A in bacteria, was detected in all 62 strains in this study. However, the prediction of antibiotic resistance genes highlighted the presence of fluoroquinolone-resistant *gyrA* in only the 21 serovar Albany strains, and none of the strains of the other two serovars. Based on this finding, the nucleotide and amino acid sequences of *gyrA* across all 62 *Salmonella enterica* strains were aligned to elucidate the differences. The sequence alignment revealed that all 21 Albany strains carried a *gyrA* mutation, specifically a Ser83 (serine at codon 83) → Phe (phenylalanine) substitution within the QRDR. Conversely, all Bareilly and Mbandaka strains possessed the wild-type *gyrA* sequence (Fig. 3). This noticeable difference highlighted that a distinct genetic feature within Albany may be attributed to a potential difference in susceptibility to quinolone antibiotics among these *Salmonella* strains.

Discussion

The pangenome represents the entire set of genes for a species rather than an individual, facilitating efficient characterization and grouping, ultimately capturing the genomic diversity within species and serovars. As depicted in Fig. 1A, three distinct groups emerged: Mbandaka (28), Albany (21), and Bareilly (13). After visualizing the pangenome, the 62 *Salmonella* strains represented three different serovars that demonstrated distinct clusters. While cgMLST on 62 strains provided insights into genetic relatedness, considering the diversity in Table 1, future studies with larger datasets are needed to confirm these findings. The two pairs of isolates within each of Bareilly (350,374) and Mbandaka (350,365) were observed to share identical cgMLST profiles at HC0 level, indicating genetic indistinguishability (Table S4). Metadata from poultry operations suggests that these isolates may have originated from the same source or experienced cross-contamination across the six processing stages in poultry operations [43]. Shared equipment or

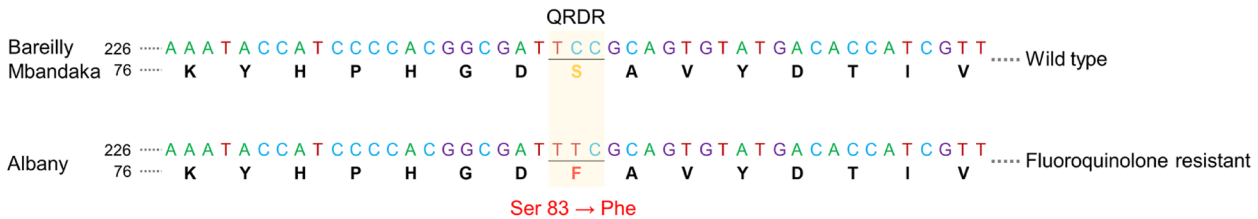


Fig. 3 Nucleotide and amino acid sequences of *gyrA* and quinolone resistance-determining regions (QRDRs) of 62 *Salmonella enterica* strains. The mutant *gyrA*, which imparts resistance to quinolone antibiotics, was detected by the protein variant model. All 21 Albany isolates in this study possessed mutant *gyrA* and the other isolates, Bareilly (13 isolates) and Mbandaka (28 isolates), possessed wild-type *gyrA*

processing surfaces are potential transmission routes that suggest further investigation.

All 62 isolates were collected from Korean poultry operations, with these three different serovars identified in this study. According to previous studies, the predominant *Salmonella enterica* subsp. serovars associated with poultry are Enteritidis, Typhimurium, and Heidelberg, while the prevalence of Infantis in poultry has been increasing [43, 44]. Similarly, another study reported traditional serotyping based on agglutination of 82 *Salmonella* strains isolated from broiler chicken farms in Brazil [45]. The results ranked *Salmonella enterica* subsp. *enterica* serovar Minnesota (40.24%), Infantis (14.63%), Heidelberg (7.31%), Senftenberg (6.09%), and Mbandaka (6.09%). Elgroud et al. found 55 *Salmonella* isolates from broiler farms and slaughterhouses, including 6 Albany (4 broilers and 2 slaughterhouses) [46]. Previous studies suggested that Albany might have free access to environments or could originate from other animal species such as poultry, cows, or sheep. One study reported from Japan identified 123 of 124 *Salmonella* isolates from broilers were Infantis [47]. According to previous studies, although Albany and Mbandaka were not predominantly found on broiler farms, they are continuously reported.

Bareilly is commonly reported worldwide from broilers and poultry-related environments including South Korea. *Salmonella* species from feces in poultry flock, dust, and eggshells were investigated in South Korea [48]. They discovered that the most frequently observed serovars were Bareilly (14), Mbandaka (11), and Rissen (6). A research investigated 325 Bareilly serovars (human cases) for approximately two years in the Czech Republic and Slovakia using a WGS method [49]. Their findings revealed around 92 cases that required hospitalization. In their study, 14 patients reported consuming chickens, eggs, ham, and yogurt, while not mentioning freshwater fish, seafood, or vegetables. The distributions of *Salmonella* serovar in this study could likely be influenced by geographic regions and other environmental factors such as climate, temperatures, agricultural practices, and animal reservoirs [50, 51]. In summary, both Mbandaka and Albany have not been frequently reported from broilers, while Bareilly is occasionally isolated from broilers and reported as a threat to public health [48, 49]. However, the identification of *Salmonella* serovars might be affected by the region and location, showing differences between diverse countries with their top different types of *Salmonella* serovar in broiler farms.

Virulence genes of three serovars were differently observed, including the presence or absence of *faeC, faeD, faeE, lpfA, lpfB, lpfC*, and *lpfE*. In particular, Bareilly and Mbandaka possessed *faeC, faeD,* and *faeE,* which are associated with adherence to *Salmonella* (fimbriae), while these virulence genes were not observed in Albany The presence of these genes was reported in Brazil, in another serovar Dublin [52], which are cattle-related, but the origin was unknown. Other researchers reported these genes in Give and Cotham, which were isolated from humans, animals, and environments in Nigeria [53]. The lpf (*lpfA, lpfB, lpfC, lpfD, lpfE*) operon encodes the long polar fimbriae proteins, which are crucial for intestinal colonization and adhesion of Typhimurium or Enteritidis [54]. However, there is very little data available on whether those fimbriae genes were observed in Albany and Mbandaka. This study may be the first report that Albany and Mbandaka isolated from chicken farm possessed these fimbriae genes (lpf operon). Likely, horizontal gene transfer events (HGT) in Typhimurium or Enteritidis played a role in transferring their genes to other serovars, including Bareilly and Mbandaka when they were in the same niches. Another interesting result is that *ratB* gene (nonfimbrial) is present in both serovars Albany and Mbandaka, but no Bareilly. This result was consistent with a prior study, indicating some *Salmonella* serovars carried *ratB* gene while others did not [55].

Several antibiotic resistance mechanisms appeared to be exclusive to Albany (Fig. 2B, Table S3). Interestingly, the presence of *aac(6')-ly* gene was exclusively observed in Bareilly in this study. This gene has been previously reported in 79 Enteritidis strains isolated from humans, poultry, and food products [56]. The activation of the *aac(6')-ly* gene in *Salmonella* plasmids pAT716 and pAT711 has been confirmed in a prior study [57]. The identification of *aac(6')-ly* in Bareilly shows a shared genetic feature with Enteritidis. Conducting a future study to investigate the presence of plasmids in Bareilly isolated in this study would contribute to a deeper understanding of their genetic mechanisms of antibiotic resistance.

The category of genes identified as antibiotic target replacement factors was uniquely observed by Albany, including *qacEdelta1, tet(D),* CARB-3 (*blaCARB-3*), and *dfrA*. Similarly, genes for antibiotic target protection (*qnrB10* and *qnrB19*) were exclusively contained in Bareilly, providing resistance by producing a protein that shields the antibiotic's target, preventing antibiotic binding. Overall, Albany expressed the highest number of antibiotic resistance genes in comparison to Bareilly and Mbandaka. This could result from the high numbers of accessory genomes in X and K categories, indicating prophages, transposons, and transcription, which may contribute to antibiotic resistance genes of Albany [58]. Transposons are mobile genetic elements capable of transfer into different locations such as plasmids, which may contain antibiotic resistance genes in a bacterium [59]. Further analysis of these findings may establish the

presence of transposons and plasmids through techniques like plasmid sequencing. Subsequent validation tests, such as PCR assay using specific primers for antibiotic resistance genes, could provide additional insights.

Albany strains in this study were found to partially carry resistance genotype variants (*bla-floR-sul1-tet(G)-dfrA1-gyrA*) reported [60]. The presence of the specific antibiotic resistance genes (*qacEdelta1, tet(D)*, CARB-3(*blaCARB-3*), *gyrA*, and *dfrA*) in Albany was able to show differences like exhibiting distinct genetic characteristics and leading to differences compared to Mbandaka and Bareilly. Additional analysis for antibiotic resistance gene variants was conducted and found a mutant *gyrA* in Albany (Fig. 3). The antibiotic resistance gene *gyrA* is a housekeeping gene found in all bacteria, encoding one of the two protein subunits of DNA gyrase, which is related to DNA replication [61]. Wild-type DNA gyrase is susceptible to the antibiotic activity of quinolone compounds [62]. However, a single point mutation within a critical region, known as the QRDR, has been found in numerous *Salmonella* serovars, conferring resistance or reduced susceptibility to quinolone antibiotics by substituting one amino acid [61, 62]. Such mutations in *gyrA* have been reported in bacteria including *Escherichia coli* and *Salmonella*, as a known cause of quinolone resistance [63]. For example, Seminati et al. reported a mutation in *gyrA* resulting in an amino acid modification within the QRDR (Ser83—> Phe) in strains of 12 different serovars of *Salmonella* [62]. However, these 12 serovars were not included among the three serovars analyzed in this current study, potentially indicating variability in resistance mechanisms across serovars. While a single *gyrA* mutation may provide initial resistance, additional mutations in this gene or the presence of plasmid-mediated quinolone resistance (PMQR) genes are often required to confer full resistance [64]. Studies have highlighted a diversity of possible substitutions leading to quinolone resistance [62, 63, 65]. These findings underscored the importance of monitoring QRDR mutations in *Salmonella* isolates to address growing threat of antibiotic resistance.

Conclusions

In this study, in silico genotyping revealed distinct serovar distributions among the 62 *Salmonella* strains, with Albany, Bareilly, and Mbandaka being predominantly isolated Korean poultry operations. Pangenome analysis highlighted genomic variability and shared characteristics within each serovar. Virulence and antibiotic resistance gene profiling demonstrated serovar-specific patterns, with Mbandaka exhibiting a higher prevalence of fimbrial adherence genes. Albany strains exhibited unique antibiotic resistance gene profiles, including fluoroquinolone resistance conferred by a *gyrA* mutation (Ser83→Phe) within the QRDR. Moreover, the presence of specific genes, such as *ratB* in Albany and *aac(6')-ly* in Bareilly, suggests potential genetic similarities with other *Salmonella* strains. The identification of mutated *gyrA* exclusively in Albany strains underscores their distinct genetic features and potential implications for antibiotic susceptibility. These findings contribute to a deeper understanding of *Salmonella* diversity, virulence, and antibiotic resistance mechanisms across different serovars, highlighting the importance of surveillance and control strategies in public health interventions. Future investigations will delve into the analysis of mobile genetic elements, including plasmids and transposons, aiming to enhance our understanding of antibiotic resistance genes.

Supplementary Information

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Supplementary Material 1.

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Authors' contributions

SP conceived and SP and HH designed research. SH collected *Salmonella* samples. SP, MK, HH, EK, and SY conducted all experiments. HH, MK, AH, HL, and SP analyzed the data and drafted the manuscript. HH, MK, and SP wrote and critically reviewed the manuscript. All authors read and approved the manuscript.

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Data availability

The 62 genomes sequenced in this study has been deposited at GenBank under the BioProject accession number PRJNA1047317.

Declarations

Ethics approval and consent to participate

This article does not contain any studies with human participants or animals performed by any of the authors.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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