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Genomic perspective of *Salmonella enterica* isolated from farm animals in Sinaloa, Mexico

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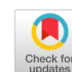

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ABSTRACT

Background: Farm animals play a crucial role as a primary source of sustenance for human consumption. However, *Salmonella* continues to be one of the major food-borne pathogens from a public health standpoint. Its persistent global concern surrounding *Salmonella* stems from its capability to induce foodborne illnesses. Unraveling the genetic characteristics of this pathogen stands as a pivotal step, shedding light on the intricate biology of *Salmonella* and aiming to mitigate its prevalence. Within this context, our study aims to delve into the genomic traits and population structure of Mexican *Salmonella* isolates derived from farm animals.
Materials and Methods: We performed next-generation sequencing across 72 genomes. Genomic data was analyzed *in silico* to determine virulence and antibiotic resistance markers. In addition, a phylogenetic tree and a spanning tree was constructed.
Results: The study revealed a diversity of 18 serovars linked to a singular ST, with prominent *S.* serovars being Oranienburg, Give, and Saintpaul. Across all isolates, an extensive array of virulence-related genes was identified. Interestingly, 95% of the isolates displayed exclusive resistance to aminoglycosides, while the remaining exhibited multidrug resistance to tetracycline and chloramphenicol. Notably, a substantial prevalence of prophages in the genomes was observed, accounting for 94% and totaling 183 sequences. The serovar Give stood out with the highest number of sequences, featuring Vibrio X29 and Escher RCS47 as the most prevalent phages.
Conclusion: This comprehensive analysis provides valuable insights into the intricate world of *Salmonella*, paving the way for enhanced understanding and targeted interventions.

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1. Introduction

Foodborne diseases persist as a globally prevalent human health concern. According to the Center for Disease Control (CDC), a complex consortium of microorganisms is responsible for 90% of illnesses, wherein *Salmonella* ranks second.[1] This gram-negative bacterium encompasses more than 2,500 serovars, categorized into typhoidal and non-typhoidal *Salmonella* based on the associated disease syndrome, affecting humans and exhibiting a wide host range.[2] Furthermore, *Salmonella* is deemed a ubiquitous bacterium, demonstrating a heightened prevalence in warm-blooded animals, notably in cattle, pigs, and poultry,[3] which function as carriage animals even in the absence of clinical manifestations.[4]

The Centers for Disease Control and Prevention (CDC) have projected an annual incidence of 1.35 million

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Salmonella infections in the United States.[5] Remarkably, Mexico mirrors this epidemiological landscape. In the year 2020 alone, 64,778 cases were reported, encompassing instances of typhoid fever (25.4%), paratyphoid (84%), and other salmonellosis (66.2%).[6] Furthermore, an examination of the past five decades in Mexico reveals a substantial surge from 7,629 to 45,280 infections. Notably, among the various Mexican states, Sinaloa holds the foremost position, exhibiting elevated rates of typhoid fever.[7]

Historically, epidemiological occurrences of *Salmonella* outbreaks have been ascribed to direct contact with animals or the ingestion of tainted animal-derived products, including meat, eggs, and milk.[8] Consequently, antibiotic administration has traditionally served as the primary therapeutic approach for treating *Salmonella* infections, albeit with adverse consequences manifested in the gradual emergence of antibiotic resistance mechanisms. Presently, the prevalence of antimicrobial resistance in *Salmonella* strains has escalated to a critical juncture, posing a significant and pressing challenge.[9]

Another noteworthy facet pertains to *Salmonella* pathogenesis, intricately linked to the expression of virulence factor genes situated within distinct pathogenicity islands (SPI).[10] A prominent component in this regard is the Type III secretion system (T3SS), recognized for its needle-like structure facilitating protein translocation within epithelial cells. This system is encoded by SPI-1 and SPI-2, playing pivotal roles in inducing cell attachment through cytoskeletal rearrangement, modulating host immune responses, ensuring intracellular survival, and facilitating invasion.[11,12]

Within this framework, a One Health approach has been advocated to investigate the interconnection among animals, the environment, and human health as primary focal points.[13] Strategic initiatives, such as next-generation sequencing and bioinformatics, have significantly expanded our understanding of the fundamental genomic characteristics of pathogens, enabling timely identification a crucial element in the intervention of foodborne outbreaks.[14] In alignment with the overarching goal of One Health, the objective of this study is to scrutinize the genomic population structure to infer certain genotypic traits associated to the Mexican isolates through the utilization of next-generation sequencing (NGS) and a bioinformatic methodology applied to *S. enterica* isolates obtained from farm animals.

2. Materials and Methods

2.1. Bacterial strains

In this study, a total of 72 *S. enterica* strains isolated from asymptomatic farm animals' manure, specifically cattle (n=38), poultry (n=17), and goat (n=17) sourced from the Culiacán Valley in Sinaloa, were employed (Table 1). The strains under investigation were procured from the private collection of the National Food Safety Laboratory (LANIIA) at the Centro de Investigación en Alimentación y Desarrollo (CIAD) in Culiacán, México. DNA extraction was conducted utilizing the DNAeasy Blood & Tissue Culture commercial kit, following the manufacturer's protocols. The concentration of the extracted DNA was quantified using the Qubit dsDNA Broad Range Assay Kit (Thermo Fisher, USA). Subsequently, the Nextera XT DNA sample kit was employed for library preparation, and genome sequencing was performed using the Illumina Miseq platform (Illumina, Inc.) to acquire paired-end reads (2x150 bp).

2.2. Reads quality control and assembly

The initial assessment of sequencing-derived reads quality was conducted using FASTQC.[15] Subsequently, Trimmomatic V0.32[16] was employed to trim sequences of suboptimal quality, defined as those falling below a Phred quality score per base of 20. Furthermore, reads with lengths less than 100 base pairs and adapters were eliminated. The *de novo* assembly of reads was accomplished through the A5-miseq pipeline[17] utilizing the paired-end reads as input. The generated assemblies were uploaded to NCBI under the PRJNA313928 BioProject.

2.3. Taxonomy and ST assignation

To validate taxonomy identity and predict sequence type (ST), the pubMLST website (REF) was used to compare *Salmonella* allelic profiles with the generated draft genomes. For serotype assignment, the stand-alone version of the *Salmonella in silico* typing resource (SISTR)[18] was employed. To visually represent the diversity in ST and locus variant, a spanning tree was generated using the online version of PHYLOViZ.[19]

Table 1: Metadata associated with the 72 genomes of *S. enterica* isolated from farm animals in the Culiacán, Sinaloa region

Genome Number	Strain Name	Country	Predicted Serotype	Isolation Source	Isolation Site
1	CA-AGO08001	Mexico	Agona	Cow	La Cofradía
2	CA-AGO08002	Mexico	Agona	Cow	La Cofradía
3	CA-TYP08001	Mexico	Typhimirium	Chicken	Agua Caliente
4	CA-ORA08006	Mexico	Oranienburg	Chicken	Jotagua
5	CA-ORA08007	Mexico	Oranienburg	Cow	Jotagua
6	CA-ORA08008	Mexico	Oranienburg	Cow	Jotagua
7	CA-ORA08002	Mexico	Oranienburg	Goat	Jotagua
8	CA-ORA08003	Mexico	Oranienburg	Chicken	Jotagua
9	CA-ORA08004	Mexico	Oranienburg	Chicken	Jotagua
10	CA-JAV09001	Mexico	Javiana	Chicken	Jotagua
11	CA-SAI08001	Mexico	Saintpaul	Cow	Jotagua
12	CA-MUE08001	Mexico	Muenchen	Cow	Jotagua
13	CA-NEW08001	Mexico	Newport	Cow	Jotagua
14	CA-WEL08001	Mexico	Weltevreden	Chicken	Jotagua
15	CA-WEL08002	Mexico	Weltevreden	Chicken	Jotagua
16	CA-WEL08003	Mexico	Weltevreden	Chicken	Jotagua
17	CA-GIV08001	Mexico	Give	Cow	Jotagua
18	CA-GIV08002	Mexico	Give	Cow	Jotagua
19	CA-ORA08001	Mexico	Oranienburg	Goat	Jotagua
20	CA-ORA08005	Mexico	Oranienburg	Chicken	Jotagua
21	CA-ORA08009	Mexico	Oranienburg	Cow	Agua Caliente
22	CA-ORA08010	Mexico	Oranienburg	Goat	La Cofradía
23	CA-ORA08011	Mexico	Oranienburg	Goat	La Cofradía
24	CA-ORA08012	Mexico	Oranienburg	Goat	La Cofradía
25	CA-ORA08013	Mexico	Oranienburg	Goat	La Cofradía
26	CA-ORA08014	Mexico	Oranienburg	Goat	La Cofradía
27	CA-ORA08015	Mexico	Oranienburg	Cow	La Cofradía
28	CA-ORA08016	Mexico	Oranienburg	Cow	La Cofradía
29	CA-ORA08017	Mexico	Oranienburg	Goat	El Castillo
30	CA-ORA08018	Mexico	Oranienburg	Goat	El Castillo
31	CA-GAM08001	Mexico	Gaminara	Cow	El Castillo
32	CA-THO08001	Mexico	Thompson	Cow	Iraguato
33	CA-THO08002	Mexico	Thompson	Cow	Iraguato
34	CA-THO08003	Mexico	Thompson	Cow	El Castillo
35	CA-ALB08001	Mexico	Albany	Chicken	Jotagua
36	CA-MON08001	Mexico	Montevideo	Goat	La Cofradía
37	CA-LUC08001	Mexico	Luciana	Cow	El Castillo
38	CA-LUC08002	Mexico	Luciana	Cow	El Castillo
39	CA-LUC08003	Mexico	Luciana	Cow	El Castillo
40	CA-NEW08002	Mexico	Newport	Cow	Iraguato
41	CA-SAI08002	Mexico	Saintpaul	Chicken	Agua Caliente
42	CA-SAI08004	Mexico	Saintpaul	Chicken	Agua Caliente
43	CA-SAI08005	Mexico	Saintpaul	Chicken	Agua Caliente
44	CA-SAI08006	Mexico	Saintpaul	Chicken	Agua Caliente
45	CA-SAI08007	Mexico	Saintpaul	Chicken	Agua Caliente
46	CA-SAI08008	Mexico	Saintpaul	Chicken	Agua Caliente
47	CA-SAI08009	Mexico	Saintpaul	Cow	Agua Caliente
48	CA-MIN08001	Mexico	Minnesota	Cow	La Cofradía
49	CA-MIN08002	Mexico	Minnesota	Cow	Iraguato
50	CA-MIN08004	Mexico	Minnesota	Cow	Iraguato

Continued on next page

Table 1 continued

51	CA-MIN08005	Mexico	Minnesota	Cow	Iraguato
52	CA-MIN08007	Mexico	Minnesota	Goat	El Castillo
53	CA-ANA08001	Mexico	Anatum	Goat	Jotagua
54	CA-ANA08002	Mexico	Anatum	Goat	Jotagua
55	CA-ANA08003	Mexico	Anatum	Goat	El Castillo
56	CA-ANA08004	Mexico	Anatum	Goat	El Castillo
57	CA-GIV09001	Mexico	Give	Goat	Jotagua
58	CA-GIV08003	Mexico	Give	Cow	Agua Caliente
59	CA-GIV08004	Mexico	Give	Cow	Agua Caliente
60	CA-GIV08005	Mexico	Give	Cow	Agua Caliente
61	CA-GIV08006	Mexico	Give	Cow	La Cofradía
62	CA-GIV08007	Mexico	Give	Cow	La Cofradía
63	CA-GIV09002	Mexico	Give	Cow	La Cofradía
64	CA-GIV08008	Mexico	Give	Cow	Iraguato
65	CA-GIV09003	Mexico	Give	Cow	El Castillo
66	CA-SAH08001	Mexico	Sahanina	Cow	El Castillo
67	CA-SAH08002	Mexico	Sahanina	Cow	El Castillo
68	CA-CAY09001	Mexico	Cayar	Cow	Jotagua
69	CA-MIN08003	Mexico	Minnesota	Cow	Iraguato
70	CA-MIN08006	Mexico	Minnesota	Goat	El Castillo
71	CA-MIN08008	Mexico	Minnesota	Cow	El Castillo
72	CA-SAI08003	Mexico	Saintpaul	Chicken	Agua Caliente

2.4. Genomic analysis

Virulence and antibiotic resistance gene annotation were conducted through the mass screening of contigs using ABRIcate.[20] This analysis incorporated the Virulence Factor Database (VFDB) and the Resfinder databases, with a selection criterion of 95% coverage and 80% alignment. Plasmid replicon detection utilized the PlasmidFinder[21] applying the aforementioned coverage and alignment parameters. The protein secretion system profile for each isolate was investigated using TXSScan with MacSyFinder.[22] Bacterial secretion systems were selected according to the fulfillment of mandatory genes for system assembly. Additionally, prophage prediction for *S. enterica* was executed using PHASTER,[23] with only intact detected prophages considered in the results. To assess genetic relatedness among isolates, a phylogenetic tree was generated based on a core alignment. Parsnp[24] employed to create the core alignment, utilizing a random reference from one of the 72 analyzed genomes. For the development of a robust and supported phylogenetic tree, RAxML[25] was utilized, employing a time-reversible GTR model with 100 bootstraps for statistical support. The resulted tree was midpoint rooted and subsequently edited using the Interactive Tree of Life iTOL.[26]

3. Results

A total of 18 *S. enterica serovars* were identified among the 72 farm animal isolates (Figure 1, panel A). The three most prevalent serovars were Oranienburg (25%), Give (15.2%), and Saintpaul (12.5%). Furthermore, a primary isolation source was found for each of the most prevalent serovars, such as Oranienburg in goat isolates, and Give and Saintpaul in cattle and poultry isolates, respectively (Figure 1, panel B). The serovars were categorized into 18 sequence types (ST) groups based on allelic profile (Figure 1, panel C). Notably, 94% of the serovars were successfully assigned to a specific ST, except for serovar Newport, designated into ST45 and ST118. STs were assigned for 92% (66 isolates) of the *S. enterica* genomes. The most frequently occurring STs were ST23 (n = 16), ST654 (n = 11), and ST50 (n = 8), corresponding to the prevalent serovars Oranienburg, Give, and Saintpaul, respectively. In terms of allelic differences, a range of 3 to 7 alleles was observed among detected STs with an average of 6 alleles.

The genomic content linked to virulence markers has been delineated across two figures. Supplementary Figure 1 illustrates the conservative profile of genes detected across all isolates while Figure 2 highlights virulence markers specific to individual serovars. Within the shared genetic framework, genes for *thin aggregative fimbriae* responsible for biofilm formation (*csgA-G*), type 1 fimbria, Type III Secretion System (T3SS) encoded by SPI-1 and SPI-2, and the TSSS-1 secreted effectors were identified in all serovars originating from the three animal sources (Figure 1). On the other hand, the related *E. coli* adhesive fimbriae (*faeC-E*) were found exclusively for the serovars Anatum, Saintpaul, Minnesota, and Oranienburg. A distinct clade, comprising five different serovars, exhibited the presence of the long polar fimbriae (*lpfA-E*). Plasmid-encoded fimbriae (pefA-D) were identified in serovar Typhimurium. The immune modulation genes *gtrA* and *gtrB* were observed in the Luciana serovar. Interestingly, the *sodCI* gene, associated with environmental stress, was present in all members of serovars Saintpaul and Weltevreden. Finally, type VI secretion system components tssJ, L, and M were found in Weltevreden and Agona serovars.

Concerning antibiotic resistance, all 72 isolates demonstrated the presence of the *aac(6´)-laa* gene, indicative of aminoglycoside antibiotic inactivation. Specifically, the *foasA7* gene associated with fosfomycin acid antibiotic resistance was found for the two *S.* Agona genomes. Additionally, *floR* and *tet(A)* genes were detected in the singular Montevideo genome, conferring resistance to phenicol and tetracycline, respectively.

A total of 58 replicon plasmids, categorized into 14 distinct types were identified among the isolates (Figure 3, panel A). Notably, the serovar Give exhibited the highest number (23/58) and diversity, encompassing 7 different replicons. The two most observed replicons were IncFII(Prsb107) and IncFII(S), with 20 and 16 occurrences, respectively, constituting 62% of the total observed replicons. The serovars Cayar, Albany, and Montevideo exhibited the lowest replicon number (1/58) and diversity (1/14).

A total of 183 prophage sequences were detected, encompassing 94% of the serovars (17/18). The highest occurrences were associated with serovars Give (46/183), Minnesota (32/183), and Oranienburg (31/183), securing the first, second, and third positions, respectively. The most frequently observed prophages across genomes were Vibrio X29 (21/183), Escher RCS47 (21/183), and Salmon Fels 1 (18/183). In contrast, Gaminara and Albany each exhibited only one prophage insertion. The least observed prophages were Entero DE3, Escher500465, Enteri Sf101, Escher 500465 1, and Entero Mu, each presenting only one sequence.

4. Discussions

The genomic diversity of *S. enterica* in farm animals from Sinaloa is composed of a broad range of 18 serovars associated with one ST. The detected serovars have been previously reported in Mexico by other investigations.[7] Nevertheless, this is the first report for serovars Thompson and Soahanina in Mexico. Similar serovars have been reported in other studies around the world in farm animals causing diarrhea.[27–29] Although the three main serovars found in this study are uncommonly related

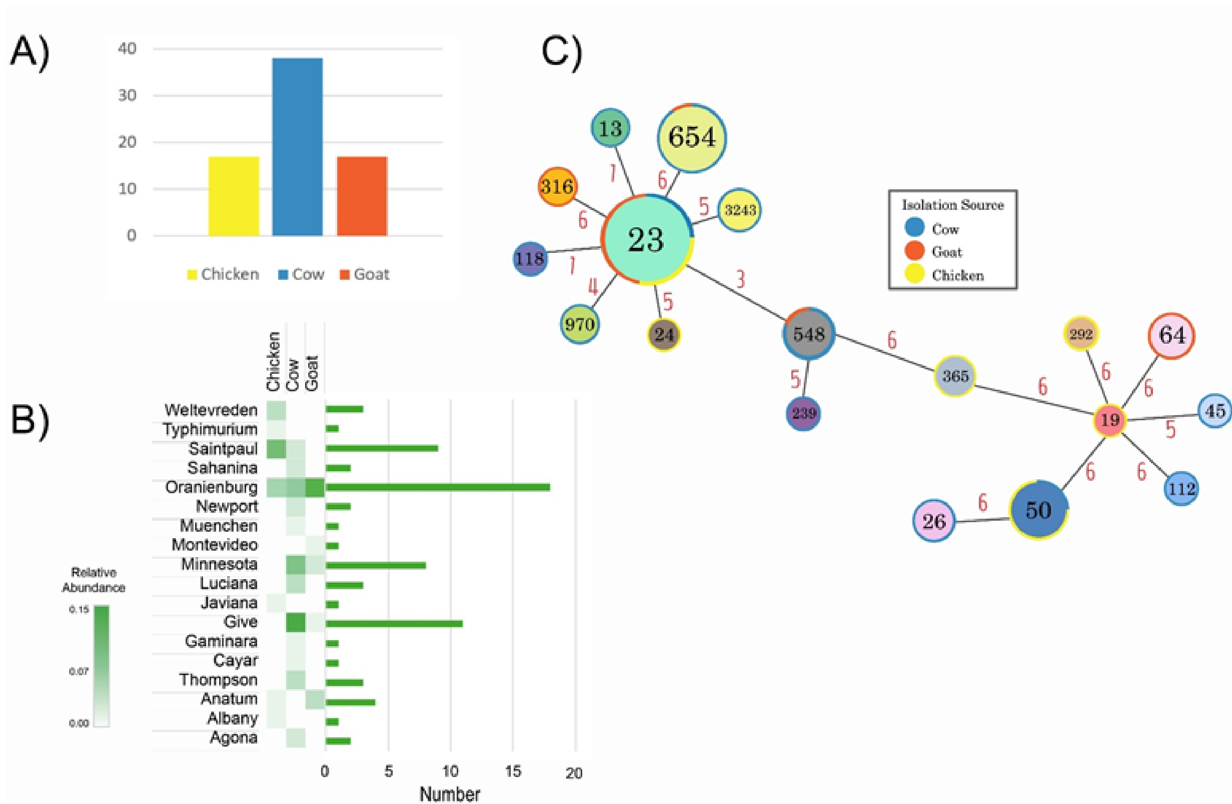

Figure 1: Distribution of *Salmonella* serovars and isolates. **A):** Number of isolates from farm animals. **B):** Distribution of *S. enterica* serovars across farm animals. **C):** Spanning tree from the 18 STs detected. Black number inside the circles represents the ST while red numbers the allelic difference among STs. Outer colored ring represents ST proportion by isolation source

to nontyphoidal salmonellosis, epidemiological outbreaks have been detected in Mexico and the rest of the world.[30–32] *Salmonella* isolates were classified into 18 STs according to the MLST. This approach consists of a typing tool for isolate comparisons, such as outbreak identification and the recognition of virulent strains.[33] Under this scenario, STs found in Sinaloa have been detected in epidemiological outbreaks in other countries. For example, STs 19 and 26 belonging to *S.* serovars Typhimurium and Thompson respectively, have been detected in patients with clinical symptoms in the USA.[34] Moreover, epidemiologic studies for serovar Agona ST13 have been related to the French and German outbreaks.[35] The resulting STs for the prevalent serovars Oranienburg (ST23), Give (ST654), and Saintpaul (ST50) support the notion of their wide distribution and prevalence in Mexico.[36,37]

The mandatory genes for T3SS assembly were found for all 72 the examined isolates. These genes facilitate the translocation of protein effectors, leading to their internalization within host cells, thereby enabling intracellular persistence and replication. Conversely, certain isolates exhibited additional virulence markers that may confer a significant advantage in terms of survival and transmission during colonization process,[38] particularly noteworthy in generalist serovars, as the predominant observed in this study. An illustrative instance is provided by the fimbria adhesive faeC-E identified in serovars, Oranienburg, Saintpaul, Minnesota, and Anatum. This fimbria notably enhances adherence to epithelial cells. Furthermore, the extensively characterized long polar fimbria may contribute to the binding of M-like cells on the intestinal Peyer patches.[39] The found *gtr* operon is accountable for the structural modification of lipopolysaccharide, potentially augmenting immune invasion by evading surface antigens recognition by the host immune system.[40] Notably, the stress adaptation *sodCl* gene may afford *Salmonella* protection against phagocytic superoxide during infection.[41] Additionally, it has been elucidated that *sodCl* plays a pivotal role in the adaptation role in *Salmonella* survival in non-host environments such river water.[42]

In contrast to findings reported in other studies,[43,44] our investigation revealed a notably low content of antibiotic resistance gene. A mere of the 95% of the examined genomes exhibited resistance to a single antibiotic, especially aminoglycoside. Conversely, the remaining 5% demonstrated multidrug resistance (MDR), encompassing resistance to tetracycline and phenicol. This discrepancy

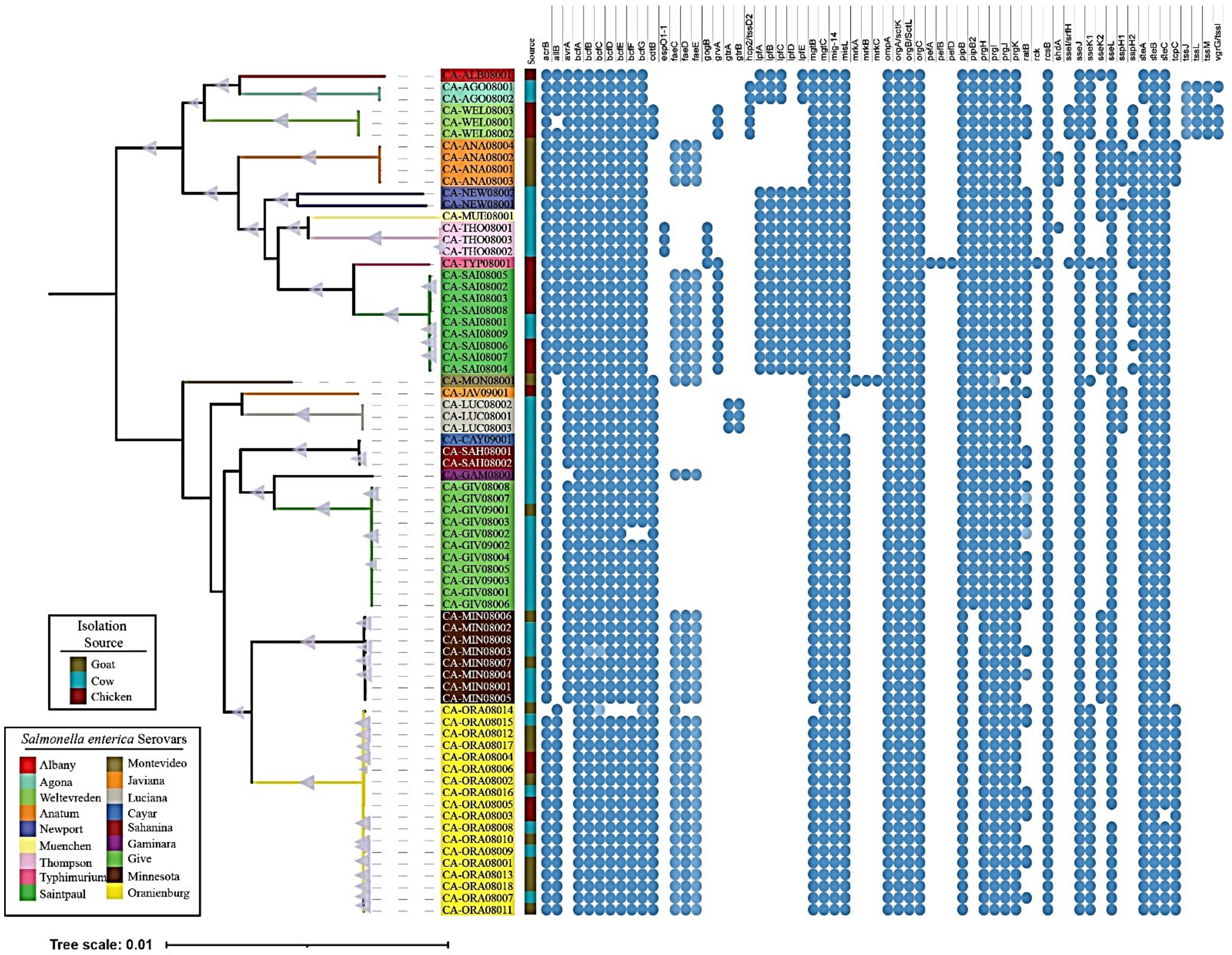

Figure 2: *S. enterica* phylogenetic tree coupled with virulence presence/absence markers. Highlighted labels show serovar. An additional color column showed sample isolation source. Specific clades are colored according serovar. Bootstraps >85 are displayed with blue triangles

may be attributed to the fact that the animals analyzed in our study originate from small-scale farms primarily dedicated to self-consumption. Consequently, the utilization of antibiotics on these farms is relatively limited. This limited usage suggests that *Salmonella* strains in this context do not readily acquire antibiotic resistance, in stark contrast to animals intended for commercialization where the indiscriminatory use of antibiotics has been implicated as a contributing factor for antibiotic resistance development.[41]

The plasmid replicons IncFII(pRSB107) and IncFII(S) emerged as the most prevalent types among the *Salmonella* isolates, a consistent finding with observations in the United States[45] and China.[46] The presence of these replicons may signify a mechanism facilitating horizontal gene transfer within *Salmonella* genomes, potentially contributing to virulence enhancement. To exemplify, IncFII(pRSB107) has been reported to harbor an aerobactin virulence marker and may be associated with MDR.[47] Additionally, the replicon Col(pHAD28) carries the qnrB19 gene, imparting quinolone resistance,[48] while IncF(S) is linked to spv, contributing to *Salmonella* systemic virulence and intramacrophage survival.[49] Prophage insertions constitute another pivotal evolutionary mechanism influencing bacterial differentiation and persistence. Notably, associations with immune protection have been established in relation to the prophage VibrioX29. This phenomenon, although infrequently observed in prior studies, was widely detected in our investigation. Furthermore, the identification of the prophages Gifsy-1, Gifsy-2, Fels-1, and Fels-2 in S. Typhimurium has been linked to an adaptative response to stress conditions.[50] Notably, studies have established that the Gifsy prophage family may genetically contribute to the presence of the

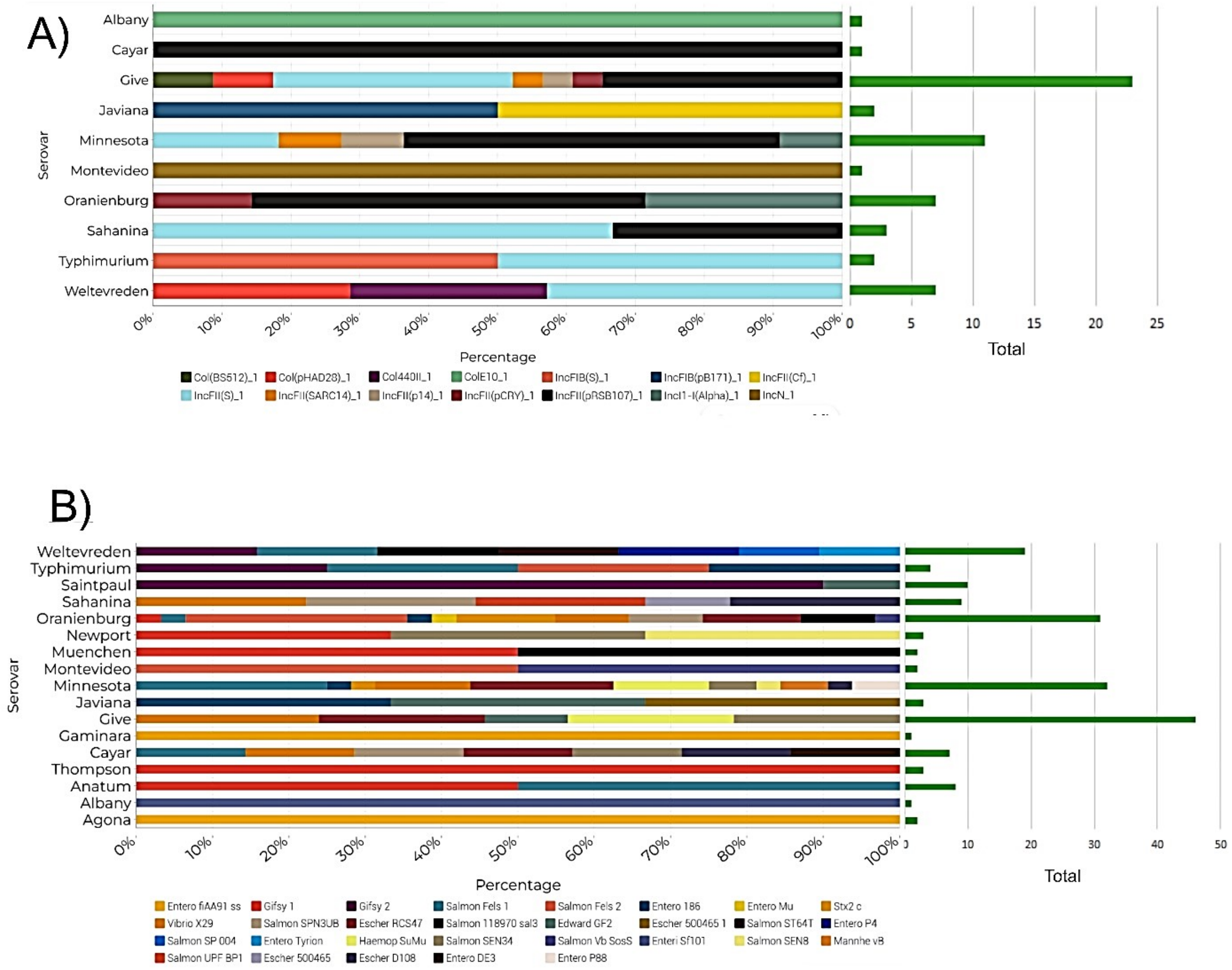

Figure 3: Accumulative graph. **A):** Graph for *Salmonella enterica* plasmids by serovar. **B):** Graph for *Salmonella enterica* phages by serovar. The serovars are shown on the Y axis, while the occurrence percentage is shown on the X axis. Each plasmid and phage are denotated with different color. Total number of plasmid or phage occurrence are shown in bar chart in green

SopE gene, facilitating host entry through membrane folding induced by cytoskeleton rearrangement.

5. Conclusions

The microcosm population structure of *Salmonella* isolated from farm animals' genomes in Sinaloa reveals 18 serovars, with *S*. Oranienburg, Give, and Saintpaul being the most prevalent. Genomic evidence related to ST outbreaks, the presence of virulence factors, and antibiotic resistance markers highlight a significant public health risk. Profiling these isolates genomically could provide invaluable association studies, aiding in tracking *Salmonella* sources and implementing timely containment measures. Replicons and prophages, acting as mechanism for horizontal gene transfer, may contribute to *Salmonella* adaptation by triggering stress responses and expanding its genomic repertoire for virulence. We advocate for an in-depth genomic characterization of replicons and prophages to enhance understanding of *Salmonella* genomic contribution to its adaptation and survival in various environments, given its ability to transition between environmental reservoirs and host. Such an approach would offer valuable insights into *Salmonella* broader ecological and adaptive potential, informing public health strategies and interventions effectively.

6. Ethics Approval and Consent to Participate

Not applicable.

7. Source of Funding

None.

8. Conflict of Interest

The authors declare no conflict of interest.

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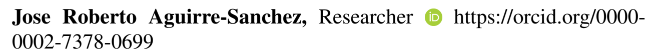
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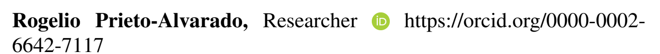
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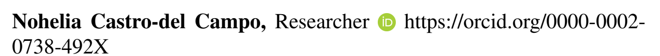
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