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ORIGINAL ARTICLE

Prophage typing of *Staphylococcus aureus* in traditional dairy products of Ilam, Iran

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ABSTRACT

Background and Objectives: Antimicrobial resistance (AMR), particularly from methicillin-resistant *Staphylococcus aureus* (MRSA), poses a significant public health threat, exacerbated by antibiotic misuse in livestock and food production. This study aimed to evaluate the prevalence of MRSA in traditional dairy products from Ilam, Iran, and explore the role of prophages in enhancing bacterial virulence and resistance, assessing their implications for food safety.

Materials and Methods: Between January and April 2021, 116 dairy samples (raw milk, traditional cheese, and toof) were collected from Ilam, Iran. *Staphylococcus aureus* was identified using bacteriological and molecular methods, including PCR targeting *femA*, *mecA*, and prophage markers (SGB, SGFa, SGFb). Antibiotic susceptibility was tested via the Kirby-Bauer method, and data were analyzed using SPSS.

Results: *S. aureus* was detected in 25.9% of samples (30/116), with raw milk showing the highest contamination (57.9%). MRSA, identified by the *mecA* gene, was present in 6.7% of isolates, and 73.3% exhibited multidrug resistance. Prophages were found in 13.3% of isolates, with SGB linked to β-lactam resistance ($p = 0.04$). High resistance to doxycycline (87%) and tetracycline (67%) was observed.

Conclusion: The study highlights a significant presence of MRSA and multidrug-resistant *S. aureus* in Ilam's dairy products, with prophages contributing to the virulence of these bacteria. Enhanced hygiene and monitoring are crucial for mitigating food safety risks.

Keywords: Methicillin-resistant *Staphylococcus aureus*; Dairy products; Prophages; Drug resistance; Food safety

INTRODUCTION

Antimicrobial resistance (AMR) is a major global health concern that has been significantly exacerbated by the excessive and inappropriate use of antibiotics in both human medicine and livestock (1). The widespread misuse of antimicrobial agents has accelerated the emergence and dissemination of resistant bacteria, compromising the effectiveness of available treatment options for infections in humans and animals alike (2). According to the World Health Organization (WHO), AMR is currently responsible for approximately 1.3 million deaths annually worldwide, with projections indicating that this number could increase to 10 million deaths per year by 2050 in the absence of effective control measures (3).

In veterinary medicine, the application of antibiotics for therapeutic purposes, disease prevention, and growth promotion in livestock plays a critical role in the selection and maintenance of antimicrobial-resis-

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tant bacteria. These resistant strains can be transmitted to humans primarily through the food chain, direct animal contact, or environmental pathways (4, 5). Among foodborne pathogens, methicillin-resistant *Staphylococcus aureus* (MRSA) is of particular concern due to its association with severe infections and its ability to persist in food production environments. MRSA has been increasingly detected in a wide range of food products, including dairy items, often as a result of inadequate hygiene during milking, processing, or handling (6, 7). Numerous studies have documented the presence of MRSA in livestock and food products, raising concerns about its potential transmission to consumers and food handlers (8, 9). These findings underscore the importance of strict hygiene practices and effective monitoring strategies throughout the food production chain to reduce public health risks (10).

The presence of MRSA in dairy products poses a significant zoonotic threat, as contaminated milk and dairy items can act as vehicles for foodborne transmission. Contamination may occur through multiple pathways, such as poor milking hygiene, colonized livestock, infected dairy workers, and cross-contamination during processing or storage (11, 12). Multiple studies have reported the presence of MRSA in raw milk and traditional dairy products, highlighting the potential for food poisoning outbreaks and difficult-to-treat infections (13, 14). Given the zoonotic nature of MRSA, transmission is particularly concerning in settings characterized by close contact between livestock and humans, such as small-scale or traditional dairy farms (15). Moreover, the detection of enterotoxigenic MRSA strains in dairy products further elevates the risk of severe foodborne illness, emphasizing the need for stringent hygiene and surveillance measures in dairy production systems (16, 17).

Previous studies have reported variable prevalence rates of MRSA in dairy products across different regions, influenced by geographic location, farming practices, and detection methodologies. A systematic review reported a pooled MRSA prevalence of 3.81% in dairy farms, with higher rates observed in Asia (4.89%) and lower rates in South America (1.33%) (18). In Egypt, MRSA was detected in 53% of dairy product samples, with raw milk exhibiting the highest contamination levels (19). In contrast, a study conducted in Great Britain reported a relatively low prevalence (2.15%) of *mecC*-positive MRSA in dairy farms, highlighting substantial regional differences (20). Factors such as milking hygiene, farm management practices, and processing conditions have been shown to significantly influence contamination rates, with poor management associated with higher MRSA prevalence (21). Additionally, the choice of detection method affects reported prevalence, as molecular techniques often reveal higher MRSA rates than conventional culture-based approaches (22). Collectively, these findings emphasize the need for region-specific surveillance and improved hygiene practices in dairy production.

Beyond antimicrobial resistance, bacterial pathogenicity is shaped by a variety of genetic elements, among which prophages—bacteriophage genomes integrated into bacterial chromosomes—play an increasingly recognized role. Prophages contribute to bacterial evolution by enhancing genetic diversity, promoting genome plasticity, and influencing host gene regulation. They may encode accessory genes, including toxins, immune evasion factors, and regulatory proteins, that enhance bacterial fitness and virulence. Evidence from diverse bacterial pathogens indicates that prophages can modulate disease severity, adaptability, and survival in hostile environments (23-26).

Prophages are also important mediators of horizontal gene transfer, facilitating the dissemination of virulence-associated traits and, in some cases, antimicrobial resistance determinants. Classic examples include Shiga toxin–encoding prophages in *Escherichia coli* O157, which are essential for its pathogenicity (27). Although plasmids and transposons are considered the primary vectors for antimicrobial resistance genes, prophages may contribute indirectly by promoting recombination events, altering regulatory networks, or co-existing with resistance determinants under selective pressure (28). In *S. aureus*, several well-characterized prophages carry genes involved in immune evasion, host adaptation, and toxin production, enhancing the bacterium's ability to persist and cause disease in both human and animal hosts (29). The widespread distribution of prophages within *S. aureus* genomes highlights their potential role in strain diversification and ecological success.

Despite growing interest in prophage biology, the extent to which prophage carriage influences antimicrobial resistance and persistence in foodborne *S. aureus* remains incompletely understood, particularly in traditional dairy settings where antimicrobial exposure and hygiene practices vary widely. Investigating prophage content alongside antimicrobial resistance profiles may therefore provide valuable insights into the genetic factors contributing to the survival and dissemination of resistant *S. aureus* strains in dairy environments.

Accordingly, the present study aimed to determine the prevalence of *Staphylococcus aureus*, including MRSA, in traditional dairy products from Ilam, Iran, and to characterize their antimicrobial resistance patterns. In addition, the study sought to detect prophage sequences in the recovered isolates and to explore their potential association with antimicrobial resistance, thereby contributing to a better understanding of *S. aureus* persistence and dissemination in dairy products.

MATERIALS AND METHODS

Study area and sampling. Between January 2021 and April 2021, a total of 116 traditional dairy product samples were collected from local retail outlets in Ilam, Iran, including raw milk (n = 38), traditional cheese (n = 39), and toof (n = 39). To note, in Iran, traditional dairy products such as "toof," a fermented dairy product prepared from dough, are widely consumed and represent a potential source of foodborne pathogens. Ilam was selected as the study area due to the high consumption of traditional dairy products and the limited availability of data regarding *S. aureus* contamination in this region.

The sample size was determined based on product availability during the study period, logistical feasibility, and consistency with previous microbiological surveys of dairy products. An approximately equal number of samples was collected for each product category to enable comparative analysis among different dairy types. Samples were obtained using a convenience sampling approach from multiple retail outlets, focusing on commonly consumed, non-industrially processed, and unpackaged products to reflect typical consumer exposure.

All samples were aseptically collected, transported to the Microbiology Laboratory of Ilam University under cold chain conditions, and stored at 4°C until microbiological analysis.

Bacteriological examination. Samples were serially diluted using phosphate buffer saline, and 1 mL of each dilution was plated on Baird-Parker agar. Plates were incubated at 37°C for 24 hours. Colonies resembling *S. aureus* (round, convex, black colonies with an opaque zone) were selected for further analysis. Isolates were identified using Gram staining and biochemical tests, including catalase, coagulase, DNase, and growth on mannitol salt agar. Isolates were stored at -20°C in 40% glycerol.

Molecular analysis. DNA was extracted from suspected S. aureus isolates following the boiling method (30). Bacterial cultures were grown in Luria-Bertani (LB) broth, centrifuged at 6000 g for 10 min twice, and the pellet was resuspended in tris-EDTA (TE) buffer. The suspension was boiled at 100°C for 5 min, centrifuged (13000 g, 5 min), and the supernatant was used as the DNA template.

PCR amplification targeting the *femA* gene was performed to confirm the identity of *S. aureus* isolates. The reaction mixture included 12.5 µL of Master Mix (Amplicon, Denmark), 1 µL of each primer (10 mM), 3 µL of template DNA, and 7.5 µL of sterile distilled water. PCR conditions were as follows: initial denaturation at 95°C for 5 min, followed by 35 cycles of denaturation at 95°C for 30 sec, annealing at 62°C for 30 sec, and extension at 72°C for 30 sec, with a final extension at 72°C for 10 min. PCR products were electrophoresed on a 1.2% agarose gel and visualized under ultraviolet light. The confirmed isolates of *S. aureus* were examined for the presence of the *mecA* and three prophage markers (SGB, SGFa, SGFb). PCR conditions (annealing temperature) for each gene were optimized according to the references provided in Table 1. Negative controls (sterile water) and positive controls (*S. aureus* ATCC 29213 for *femA* and ATCC 33591^T for *mecA*) were included in all PCR runs.

Antibiotic susceptibility testing. Antibiotic resistance patterns were determined using the Kirby-Bauer disk diffusion method following Clinical and Laboratory Standards Institute (CLSI, 2022) guidelines (34). A standardized 0.5 McFarland suspension of each isolate was lawn-cultured on Mueller-Hinton agar (Himedia, India).

Ten antibiotic disks representing six major classes were applied: penicillin G (10 units), amoxicillin (20 µg), oxacillin (1 µg), cefoxitin (30 µg), doxycycline (30 µg), tetracycline (30 µg), cefixime (5 µg), cefotaxime (30 µg), vancomycin (30 µg), and imipenem (10

Table 1. List of oligonucleotide primers used in the study

Target gene/phage	Primer sequence (5'-3')	Amplicon size (bp)	Annealing temperature (°C)	Reference
femA	AAAATCGATGGTAAAGGTTGG	450	60	(31)
	AGTTCTGCACTACCGGATTTGC			
mecA	CGATCCATATTTACCATATCA	533	62	(32)
	ATCACGCTCTTCGTTTAGTT			
SGB	ACTTATCCAGGTGGYGTTATTG	405	58	(33)
	TGTATTTAATTTCGCCGTTAGTG			
SGFa	TACGGGAAAATATTCGGAAG	548	58	(33)
	ATAATCCGCACCTCATTCCT			
SGFb	AGACACATTAAGTCGCACGATAG	147	58	(33)
	TCTTCTCTGGCACGGTCTCTT			

μg). After incubation at 35°C for 24 hours, inhibition zone diameters were measured to the nearest millimeter according to CLSI breakpoints. Quality control was performed weekly using *S. aureus* ATCC 25923.

Statistical analysis. Data were analyzed using SPSS software (version 19.0). Descriptive statistics were used to summarize the results, including frequencies and percentages for the prevalence of resistance genes and antibiotic resistance patterns.

RESULTS

Isolation of *S. aureus.* A total of 116 dairy samples were analyzed, comprising raw milk (n = 38), traditional cheese (n = 39), and toof (n = 39). Among these, *S. aureus* was detected in 30 samples (25.9%) using culture-based methods and biochemical tests. The isolates were distributed as follows: 22 (57.9%) from raw milk, 3 (7.7%) from traditional cheese, and 5 (12.8%) from toof. These findings indicate that raw milk had the highest contamination rate, followed by toof and traditional cheese. The distribution of *S. aureus*-positive samples across different dairy products is detailed in Table 2.

Virulence and resistance genes. The *femA* gene, a species-specific marker for *S. aureus*, was detected in all 30 (100%) isolates (Fig. 1). Among the 30 *S. aureus* isolates, 2 (6.7%) carried the *mecA* gene, indicating methicillin resistance (MRSA) (Fig. 2). The presence of *mecA* highlights the potential for these isolates to cause difficult-to-treat infections, particularly in immunocompromised individuals.

Prophage carriage and potential for horizontal gene transfer. Prophage-associated genetic sequences were detected in a subset of *S. aureus* isolates using PCR targeting conserved bacteriophage genes. Using genomic DNA as the amplification template, markers corresponding to the SGB prophage group were detected in 6.7% (2/30) of isolates, while SGFa and SGFb prophage markers were each identified in 3.3% (1/30) of isolates (Figs. 3A-C).

Antibiotic susceptibility profiling. Antimicrobial susceptibility testing revealed high resistance rates among *S. aureus* isolates, notably to doxycycline (87%) and tetracycline (67%). In contrast, low resistance was observed to imipenem (3%) and cefazolin (5.6%). Intermediate susceptibility was common for several β-lactam antibiotics, including cefazolin (80%) and oxacillin (50%).

Multidrug resistance (MDR), defined as resistance to three or more antimicrobial classes, was identified in 73.3% (22/30) of the isolates (Table 3).

Association between prophage presence and antibiotic resistance. The relationship between prophage carriage and antimicrobial resistance was evaluated using the chi-square (χ^2) test or Fisher's exact test, as appropriate. Isolates harboring prophage sequences exhibited higher resistance rates to tetracyclines and cephalosporins compared with prophage-negative isolates; however, these differences were not statistically significant ($P > 0.05$). No statistically significant association was observed between prophage presence and methicillin resistance or multidrug resistance status.

Table 2. Distribution of *S. aureus* isolates in dairy products

Dairy Product	Number of Samples	Number of *S. aureus* isolates	Percentage of *S. aureus* isolates
Raw milk	38	22	57.9%
Traditional cheese	39	3	7.7%
Toof	38	5	12.8%
Total	116	30	25.9%

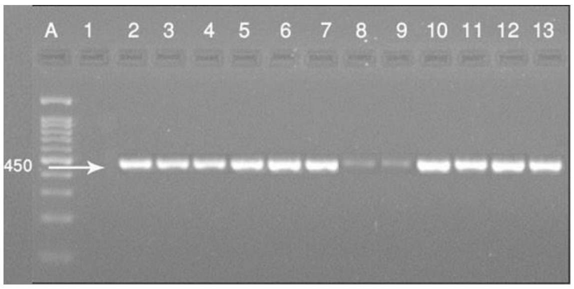


Fig. 1. Agarose gel electrophoresis of *femA* gene PCR products.
Lanes: A) DNA size marker (100 bp ladder); 1) Negative control; 2) *S. aureus* (ATCC 29213); 3-13) PCR products from *S. aureus* isolates.

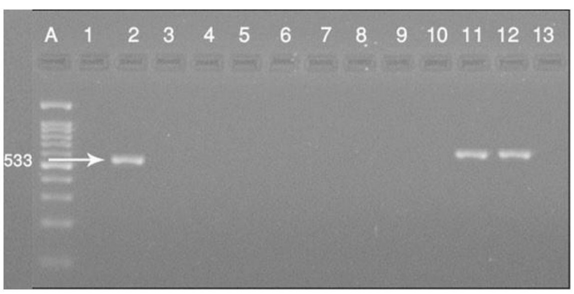
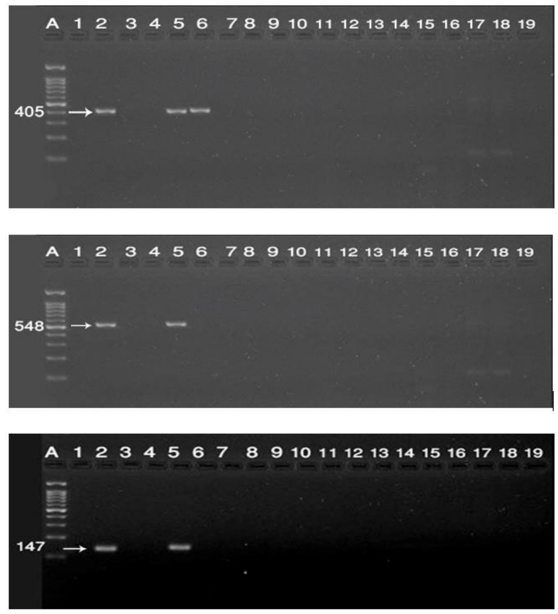


Fig. 2. Agarose gel electrophoresis of *mecA* gene PCR products.
Lanes: A) DNA size marker (100 bp ladder); 1) Negative control; 2) *S. aureus* (ATCC 33591T); 3-13) PCR products from *S. aureus* isolates.

A



B

C

Fig. 3. Agarose gel electrophoresis of prophage markers PCR products.
A: Lanes: A) DNA size marker (100 bp ladder); 1) Negative control; 2) *S. aureus* (ATCC 33591T); 3-19) PCR products from *S. aureus* isolates (SGB, 405 bp).
B: Lanes: A) DNA size marker (100 bp ladder); 1) Negative control; 2) *S. aureus* (ATCC 33591T); 3-19) PCR products from *S. aureus* isolates (SGFa, 548 bp).
C: Lanes: A) DNA size marker (100 bp ladder); 1) Negative control; 2) *S. aureus* (ATCC 33591T); 3-19) PCR products from *S. aureus* isolates (SGFb, 147 bp).

Table 3. Antibiotic resistance profiles of *S. aureus* isolates

Family	Antibiotic	Resistant (%)	Intermediate (%)	Sensitive (%)
Penicillins	Penicillin G	16	47	37
Cephalosporins	Cefazolin	5.6	80	13.5
	Cefotaxime	43	24	33
	Cefixime	57	37	6
Carbapenems	Imipenem	3	3	94
Glycopeptides	Vancomycin	13	53	34
Piperacillins	Amoxicillin	10	37	53
	Oxacillin	13	50	37
Tetracyclines	Tetracycline	67	30	3
	Doxycycline	87	6.5	6.5

DISCUSSION

This study aimed to assess the prevalence of *S. aureus*, particularly MRSA, in traditional dairy products—raw milk, traditional cheese, and toof—from Ilam, Iran, and to investigate the potential role of prophages in bacterial virulence, especially regarding their contribution to antibiotic resistance. Overall, *S. aureus* was detected in 25.9% of samples, with raw milk showing the highest contamination rate (57.9%), followed by toof (12.8%) and traditional cheese (7.7%). These findings align with previous reports indicating that raw milk is more frequently contaminated than processed dairy products due to limited heat treatment and handling practices (12).

MRSA was identified in 6.7% of isolates, all carrying the *mecA* gene, a key determinant of methicillin resistance. The presence of MRSA in traditional dairy products poses a significant public health concern, as consuming contaminated products may facilitate the community spread of resistant strains and complicate infection treatment (35, 36). Additionally, the possibility of zoonotic transmission of antibiotic resistance genes from livestock to humans highlights the need for vigilant monitoring and strict hygiene practices in dairy production and handling (16).

Comparative analyses with other studies reveal notable regional differences in MRSA prevalence. A systematic review reported a pooled prevalence of 3.81% globally in dairy farms, with Asia-specific rates at 4.89% (18). The higher prevalence observed in Ilam may reflect local farming practices, hygiene standards, and patterns of antibiotic use, which differ from those in other regions (11, 13). In Egypt, MRSA prevalence in dairy products has ranged widely from 3% to 53%, influenced by product type and local handling procedures (19, 37). Similarly, studies have documented contamination on the hands of dairy workers, indicating additional potential transmission routes (38). In contrast, research from northwestern Italy reported only a 2% prevalence of MRSA in bulk tank milk from goat farms, demonstrating considerable variability across regions and production systems (39). These differences highlight the importance of local interventions and ongoing monitoring to reduce foodborne MRSA transmission (40, 41).

Antimicrobial resistance profiling showed high resistance rates to tetracycline (67%) and doxycycline (87%), reflecting their extensive use in livestock for growth promotion and disease prevention. Multidrug resistance was found in 73.3% of isolates, in line with previous reports of high MDR prevalence in *S. aureus* from dairy products. Although prophage-positive isolates tended to show higher resistance frequencies, statistical analysis using chi-square and Fisher's exact tests revealed no significant link between prophage carriage and antimicrobial resistance ($P > 0.05$). This suggests that prophages may contribute indirectly to bacterial adaptation and fitness rather than acting as primary carriers of resistance genes, with plasmids, transposons, and selective antibiotic pressure playing more direct roles in resistance development.

Prophages, especially SGB and φSa3 groups, are known to play vital roles in *S. aureus* virulence. φSa3 prophages encode immune evasion genes and can disrupt the β-hemolysin (*hlb*) gene, enhancing bacterial survival in host environments (42, 43). SGB prophages were identified in several isolates showing higher β-lactam resistance, although the link was not statistically significant. The observed trend may reflect indirect mechanisms such as co-selection under antibiotic pressure, promotion of genetic plasticity, or co-localization with resistance genes on mobile elements like SCC*mec* (28). These findings support previous research showing that prophages can indirectly influence antimicrobial resistance by facilitating horizontal gene transfer, recombination, and genomic diversity, ultimately boosting bacterial fitness in foodborne environments (44).

The high prevalence of MDR and tetracycline resistance highlights the selective pressure from routine antibiotic use in local dairy farms. While prophages are not direct carriers of resistance genes in this study, they may support the persistence of resistant strains by promoting genetic diversity and adaptability. This underscores the need for integrated strategies that address both antimicrobial use and mobile genetic elements involved in bacterial survival within food production systems.

This study's results emphasize the importance of strict food safety measures in traditional dairy production. Implementing enhanced hygiene practices during milking, handling, and processing—especially for raw milk—is vital to reduce contamination risks. Establishing continuous surveillance programs to monitor antimicrobial resistance trends and emerging issues is crucial for timely public health responses (45-47). These strategies align with global One Health goals, stressing the interconnectedness of human, animal, and environmental health, and support sustainable agricultural practices and food security in regions where traditional dairy consumption is common (48, 49).

Several limitations should be considered when interpreting these findings. Although 116 dairy samples were collected, only 30 *S. aureus* isolates were available for detailed antimicrobial resistance and prophage analysis, possibly limiting statistical power and the ability to find significant associations. The cross-sectional design prevents assessment of seasonal or temporal trends, and focusing on a single region may limit the applicability of findings to other areas with different farming and antibiotic use practices. PCR-based detection methods might have missed low-abundance or highly divergent prophages, and the absence of whole-genome sequencing limited detailed characterization of prophage-encoded genes. Despite the collection period being in 2021, the results remain relevant, as resistance patterns to commonly used antibiotics continue to persist in the region, providing a snapshot of ongoing antimicrobial pressures in traditional dairy systems.

Future research should prioritize longitudinal studies to track seasonal and temporal variations in contamination and resistance patterns. Expanding geographic sampling to include multiple regions would enhance generalizability and allow comparative analyses. Applying whole-genome sequencing could offer a more comprehensive understanding of prophage diversity and associated virulence and resistance genes, clarifying their evolutionary roles. Additionally, examining how specific production practices influence contamination and resistance rates could help develop targeted interventions, while combining microbiological and epidemiological data would strengthen public health strategies to mitigate risks from foodborne pathogens.

CONCLUSION

The detection of methicillin-resistant and multidrug-resistant *S. aureus* in traditional dairy products highlights the importance of routine microbiological surveillance, particularly for raw milk. The observed resistance patterns support the need for targeted antimicrobial monitoring programs in dairy production systems. These findings may assist regulatory authorities in refining food safety monitoring strategies and inform public health policies aimed at reducing the risk of foodborne transmission of resistant *S. aureus.*

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REFERENCES

1. Cella E, Giovanetti M, Benedetti F, Scarpa F, Johnston C, Borsetti A, et al. Joining forces against antibiotic resistance: The one health solution. *Pathogens* 2023; 12: 1074.
2. Ifedinezi OV, Nnaji ND, Anumudu CK, Ekwueme CT, Uhegwu CC, Ihenetu FC, et al. Environmental antimicrobial resistance: implications for food safety and public health. *Antibiotics (Basel)* 2024; 13: 1087.
3. Di Pietro M, Filardo S, Sessa R. Editorial for the special issue "Antibacterial activity of drug-resistant strains". *Int J Mol Sci* 2024; 25: 1878.
4. Lekshmi M, Ammini P, Kumar S, Varela MF. The food production environment and the development of antimicrobial resistance in human pathogens of animal origin. *Microorganisms* 2017; 5: 11.
5. Clifford K, Desai D, da Costa CP, Meyer H, Klohe K, Winkler AS, et al. Antimicrobial resistance in livestock and poor-quality veterinary medicines. *Bull World Health Organ* 2018; 96: 662-664.
6. Hennekinne JA, De Buyser ML, Dragacci S. *Staphylococcus aureus* and its food poisoning toxins: characterization and outbreak investigation. *FEMS Microbiol Rev* 2012; 36: 815-836.
7. Zhang Z, Liu W, Xu H, Aguilar ZP, Shah NP, Wei H. Propidium monoazide combined with real-time PCR for selective detection of viable *Staphylococcus aureus* in milk powder and meat products. *J Dairy Sci* 2015; 98:1625-1633.
8. Klimešová M, Manga I, Nejeschlebová L, Horáček J, Ponížil A, Vondrušková E. Occurrence of *Staphylococcus aureus* in cattle, sheep, goat, and pig rearing in the Czech Republic. *Acta Vet Brno* 2017; 86: 3-10.
9. Jackson CR, Davis JA, Barrett JB. Prevalence and characterization of methicillin-resistant *Staphylococcus aureus* isolates from retail meat and humans in Georgia. *J Clin Microbiol* 2013; 51: 1199-1207.
10. Ou C, Shang D, Yang J, Chen B, Chang J, Jin F, et al. Prevalence of multidrug-resistant *Staphylococcus*

aureus isolates with strong biofilm formation ability among animal-based food in Shanghai. *Food Control* 2020; 112: 107106.
11. Schnitt A, Tenhagen B. Risk factors for the occurrence of Methicillin-Resistant *Staphylococcus aureus* in dairy herds: an update. *Foodborne Pathog Dis* 2020; 17: 585-596.
12. Titouche Y, Hakem A, Houali K, Meheut T, Vingadassalon N, Ruiz-Ripa L, et al. Emergence of methicillin-resistant *Staphylococcus aureus* (MRSA) ST8 in raw milk and traditional dairy products in the Tizi Ouzou area of Algeria. *J Dairy Sci* 2019; 102: 6876-6884.
13. Titouche Y, Akkou M, Houali K, Auvray F, Hennekinne JA. Role of milk and milk products in the spread of methicillin-resistant *Staphylococcus aureus* in the dairy production chain. *J Food Sci* 2022; 87: 3699-3723.
14. Riva A, Borghi E, Cirasola D, Colmegna S, Borgo F, Amato E, et al. Methicillin-Resistant *Staphylococcus aureus* in Raw Milk: Prevalence, SCC*mec* Typing, Enterotoxin Characterization, and Antimicrobial Resistance Patterns. *J Food Prot* 2015; 78: 1142-1146.
15. Lienen T, Schnitt A, Cuny C, Maurischat S, Tenhagen BA. Phylogenetic tracking of LA-MRSA ST398 intra-farm transmission among animals, humans and the environment on German dairy farms. *Microorganisms* 2021; 9: 1119.
16. Zhang Z, Wang J, Wang H, Zhang L, Shang W, Li Z, et al. Molecular surveillance of MRSA in raw milk provides insight into MRSA cross species evolution. *Microbiol Spectr* 2023; 11(4): e0031123.
17. Alkuraythi DM, Alkhulaifi MM. Methicillin-resistant *Staphylococcus aureus* prevalence in food-producing animals and food products in Saudi Arabia: A review. *Vet World* 2024; 17: 1753-1764.
18. Khanal S, Boonyayatra S, Awaiwanont N. Prevalence of methicillin-resistant *Staphylococcus aureus* in dairy farms: A systematic review and meta-analysis. *Front Vet Sci* 2022; 9: 947154.
19. Al-Ashmawy MA, Sallam KI, Abd-Elghany SM, Elhadidy M, Tamura T. Prevalence, Molecular characterization, and antimicrobial susceptibility of methicillin-resistant *Staphylococcus aureus* isolated from milk and dairy products. *Foodborne Pathog Dis* 2016; 13: 156-162.
20. Paterson GK, Morgan FJ, Harrison EM, Peacock SJ, Parkhill J, Zadoks RN, et al. Prevalence and properties of *mecC* methicillin-resistant *Staphylococcus aureus* (MRSA) in bovine bulk tank milk in Great Britain. *J Antimicrob Chemother* 2014; 69: 598-602.
21. Tegegne H, Ejigu E, Woldegiorgis D, Mengistu A. Isolation and antimicrobial resistance patterns of methicillin-resistant *Staphylococcus aureus* from raw cow's milk in dairy farms of Wolaita Sodo Town, Southwest, Ethiopia. *Food Sci Nutr* 2024; 12: 4735-4744.
22. Ou Q, Zhou J, Lin D, Bai C, Zhang T, Lin J, et al. A large meta-analysis of the global prevalence rates of *S. aureus* and MRSA contamination of milk. *Crit Rev Food Sci Nutr* 2018; 58: 2213-2228.
23. Magaziner SJ, Zeng Z, Chen B, Salmond GP. The Prophages of *Citrobacter rodentium* represent a conserved family of horizontally acquired mobile genetic elements associated with enteric evolution towards pathogenicity. *J Bacteriol* 2019; 201(9): e00638-18.
24. Patel PH, Maxwell KL. Prophages provide a rich source of antiphage defense systems. *Curr Opin Microbiol* 2023; 73: 102321.
25. Varani AM, Monteiro-Vitorello CB, Nakaya HI, Van Sluys MA. The role of prophage in plant-pathogenic bacteria. *Annu Rev Phytopathol* 2013; 51: 429-451.
26. Vale FF, Roberts RJ, Kobayashi I, Camargo MC, Rabkin CS, HpGP Research Network. Gene content, phage cycle regulation model and prophage inactivation disclosed by prophage genomics in the *Helicobacter pylori* Genome Project. *Gut Microbes* 2024; 16: 2379440.
27. Asadulghani MD, Ogura Y, Ooka T, Itoh T, Sawaguchi A, Iguchi A, et al. The defective prophage pool of *Escherichia coli* O157: Prophage–prophage interactions potentiate horizontal transfer of virulence determinants. *PLoS Pathog* 2009; 5(5): e1000408.
28. Kondo K, Kawano M, Sugai M. Distribution of antimicrobial resistance and virulence genes within the prophage-associated regions in nosocomial pathogens. *mSphere* 2021; 6(4): e0045221.
29. Nepal R, Houtak G, Shaghayegh G, Bouras G, Shearwin K, Psaltis AJ, et al. Prophages encoding human immune evasion cluster genes are enriched in *Staphylococcus aureus* isolated from chronic rhinosinusitis patients with nasal polyps. *Microb Genom* 2021; 7: 000726.
30. Tavarideh F, Pourahmad F, Nemati M. Diversity and antibacterial activity of endophytic bacteria associated with medicinal plant, *Scrophularia striata*. *Vet Res Forum* 2022; 13: 409-415.
31. Adeyemi FM, Oyedara OO, Yusuf-Omoloye NA, Ajigbewu OH, Ndaji OL, Adegbite-Badmus MK, et al. Guardians of resistance and virulence: detection of *mec*, *femA*, *Van*, *pvl*, *hlg* and *spa* genes in methicillin and vancomycin-resistant *Staphylococcus aureus* from clinical and food samples in Southwestern Nigeria. *BMC Microbiol* 2024; 24: 498.
32. Kobayashi N, Wu H, Kojima K, Taniguchi K, Urasawa S, Uehara N, et al. Detection of *mecA*, *femA*, and *femB* genes in clinical strains of staphylococci using polymerase chain reaction. *Epidemiol Infect* 1994; 113: 259-266.
33. Pantůček R, Doškař J, Růžičková V, Kašpárek P, Oráčová E, Kvardová V, et al. Identification of bacte-

riophage types and their carriage in *Staphylococcus aureus*. *Arch Virol* 2004; 149: 1689-1703.
34. CLSI (2022). Performance standards for antimicrobial susceptibilitytesting.In:CLSIsupplementM100.32nded. Clinical and Laboratory Standards Institute, Wayne, PA. https://clsi.org/shop/standards/m100/ (Accessed on 1/17/2024).
35. Dehkordi NV, Rahimi E, Jahromi NZ. Prevalence, antimicrobial resistance, virulence gene distribution and SCC*mec* typing of methicillin-resistant *Staphylococcus aureus* isolated from raw milk and dairy products. *Iran J Microbiol* 2024; 16: 605-613.
36. Lemma F, Alemayehu H, Stringer A, Eguale T. Prevalence and antimicrobial susceptibility profile of *Staphylococcus aureus* in milk and traditionally processed dairy products in Addis Ababa, Ethiopia. *Biomed Res Int* 2021; 2021: 5576873.
37. Sadat A, Shata RR, Farag AM, Ramadan H, Alkhedaide A, Soliman MM, et al. Prevalence and characterization of *pvl*-positive *Staphylococcus aureus* isolated from raw cow's milk. *Toxins (Basel)* 2022; 14: 97.
38. Vandendriessche S, Vanderhaeghen W, Soares FV, Hallin M, Catry B, Hermans K, et al. Prevalence, risk factors and genetic diversity of methicillin-resistant *Staphylococcus aureus* carried by humans and animals across livestock production sectors. *J Antimicrob Chemother* 2013; 68: 1510-1516.
39. Locatelli C, Cremonesi P, Caprioli A, Carfora V, Ianzano A, Barberio A, et al. Occurrence of methicillin-resistant *Staphylococcus aureus* in dairy cattle herds, related swine farms, and humans in contact with herds. *J Dairy Sci* 2017; 100: 608-619.
40. Cortimiglia CE, Bianchini V, Franco A, Caprioli A, Battisti A, Colombo L, et al. Short communication: prevalence of *Staphylococcus aureus* and methicillin-resistant *S. aureus* in bulk tank milk from dairy goat farms in Northern Italy. *J Dairy Sci* 2015; 98: 2307-2311.
41. Algammal AM, Enany ME, El-Tarabili RM, Ghobashy MO, Helmy YA. Prevalence, antimicrobial resistance profiles, virulence and enterotoxins-determinant genes of MRSA isolated from subclinical bovine mastitis in Egypt. *Pathogens* 2020; 9: 362.
42. Nepal R, Houtak G, Bouras G, Feizi S, Shaghayegh G, Shearwin K, et al. A φSa3int (NM3) prophage domestication in *Staphylococcus aureus* leads to increased virulence through human immune evasion. *MedComm* (2020) 2025; 6(8): e70313.
43. Rohmer C, Wolz C. The role of *hlb*-converting bacteriophages in *Staphylococcus aureus* host adaption. *Microb Physiol* 2021; 31: 109-122.
44. Tran PM, Feiss M, Kinney KJ, Salgado-Pabón W. ϕSa3mw prophage as a molecular regulatory switch of *Staphylococcus aureus* β-toxin production. *J Bacteriol* 2019; 201(14): e00766-18.
45. Zhu Z, Wu S, Chen X, Tan W, Zou G, Huang Q, et al. Heterogeneity and transmission of food safety-related enterotoxigenic *Staphylococcus aureus* in pig abattoirs in Hubei, China. *Microbiol Spectr* 2023; 11(5): e0191323.
46. Guo H, Pan L, Li L, Lu J, Kwok L, Menghe B, et al. Characterization of antibiotic resistance genes from *Lactobacillus* isolated from traditional dairy products. *J Food Sci* 2017; 82: 724-730.
47. Kerek Á, Németh V, Szabó Á, Papp M, Bányai K, Kardos G, et al. Monitoring changes in the antimicrobial-resistance gene set (ARG) of raw milk and dairy products in a cattle farm, from production to consumption. *Vet Sci* 2024; 11: 265.
48. Adnyana IM, Utomo B, Eljatin DS, Sudaryati NL. One Health approach and zoonotic diseases in Indonesia: Urgency of implementation and challenges. *Narra J* 2023; 3(3): e257.
49. Da Cunha DT. Improving food safety practices in the foodservice industry. *Curr Opin Food Sci* 2021; 42: 127-133.