Published Online: 2025 June 7 **Review Article**

A Comprehensive Review on *Staphylococcus aureus* Complex, with Emphasis on *S. argenteus*, *S. roterodami*, *S. schweitzeri*, *S. singaporensis*, and Their Role in Human Infections

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Abstract

Context: The *Staphylococcaceae* family consists of nine genera, with *Staphylococcus* being one of them. In 2015, the *Staphylococcus aureus* complex was introduced, incorporating five species: *Staphylococcus aureus*, *S. roterodami*, *S. argenteus* (formerly identified as *S. aureus* clonal complex 75 or CC75), *S. schweitzeri*, and *S. singaporensis*.

Evidence Acquisition: This review comprehensively examines the *S. aureus* complex, particularly focusing on lesser-known and overlooked species.

Results: This article highlights their important roles in human infections and food safety, which have been underexplored. This review explains updated taxonomic classifications and emphasizes these species' distinct phenotypic and molecular characteristics.

Conclusions: Additionally, we discuss their clinical manifestations, virulence factors, and antibiotic resistance patterns for readers and clinicians.

Keywords: *Staphylococcus*, *Staphylococcus aureus* Complex, Pathogenesis, Antibiotic Resistance, Food Poisoning

1. Context

The *Staphylococcaceae* family received approval in 2009 (1, 2), encompassing nine genera (3). Ogston's original description in 1883 introduced the genus *Staphylococcus* (4, 5). Later, Rosenbach further classified this genus into *Staphylococcus* albus and *Staphylococcus aureus* (4, 6). In 1886, Flügge distinguished *Staphylococcus* from *Micrococcus* (4, 7), emphasizing differences in DNA G+C content: 33 - 40 mol% for *Staphylococcus* species and approximately 70 mol% for *Micrococcus* species (4). The validation of the *Staphylococcus* genus was ultimately confirmed in 1980 (8, 9). *Staphylococcus* is a member of the Domain Bacteria, Kingdom Bacillati, Phylum Bacillota, Class Bacilli, Order Caryophanales, and Family *Staphylococcaceae* (10). This genus is the most prevalent member of this family (11). Up to the present time, the *S. aureus* complex comprises *S. aureus*, *S. roterodami*, *S. argenteus* (formerly identified as *S. aureus* clonal complex 75 or CC75) (12), *S. schweitzeri*, and *S. singaporensis*, playing an essential role in infections affecting both humans and animals. The cell wall structure and chemical composition of *Staphylococcus* species closely resemble those of other Gram-positive bacteria. Peptidoglycan, protein, and teichoic acid constitute the cell wall of this group of bacteria (13). In some species, the peptidoglycan type is Lys-Gly5–6, and teichoic acids consist of glycerol, ribitol, and N-acetylamino sugars (4). Additionally, the notable fatty acids in *S. roterodami* are anteiso-C15:0, anteiso-C17:0, and iso-C15:0 (14). The current article emphasizes that this review distinctly focuses on the lesser-known and overlooked members of the *S. aureus* complex,

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particularly *S. argenteus*, *S. roterodami*, *S. schweitzeri*, and *S. singaporensis*. Unlike previous review articles that predominantly focused on *S. aureus*, our article surveyed recent taxonomic updates, virulence factors, and antibiotic resistance profiles specific to these species. Previous studies reported *S. argenteus*, *S. aureus*, *S. roterodami*, and *S. singaporensis* from human infections (15, 16). Additionally, we emphasize their important roles in clinical infections and food safety, which have not been addressed enough in the literature. By providing a comprehensive review of existing knowledge and emphasizing the clinical manifestation and epidemiological implications of these species, our review aims to fill important and vital gaps and inspire further research in this field.

2. Isolation from Human Clinical Specimens

Staphylococcus species, especially *S. aureus*, is a frequent source of various infections in hospitals and the community (17). These bacteria can be isolated from various clinical specimens such as a catheter (18) and skin (4, 19-21) [The swab technique is suitable for isolation (22), and the plate should be incubated at 34 - 35°C for 72 to 96 hours]. Additionally, it can be isolated from sepsis and blood culture (21, 23-25), body fluids (4, 24), joints [joint aspirate and/or intraoperative tissue samples are isolated and cultured on selective media] (24, 26), ocular sources (4, 27), sputum (21), ears (19, 21), and urine when there are 100,000 bacterial cells or more per mL in a midstream specimen. However, this criterion varies in different references. The urine specimen is homogenized, and the loop is vertically introduced into the bottle. The specimen is then seeded onto a blood agar (BA) medium and incubated for 18 to 24 hours at a temperature of 35°C (4, 28), as routinely performed in clinical laboratories. Some data are presented in Table 1. Typically, this genus is isolated on sheep BA in the primary culture within 18 - 24 hours (4). Various selective media isolate *Staphylococcus* from stool specimens and similar samples like nasal and skin specimens. These include Columbia CNA agar (containing blood, colistin, nalidixic acid) (29), lipase-salt-mannitol agar, mannitol salt agar (30, 31), phenylethyl alcohol agar (containing pancreatic digest of casein, papic digest of soybean meal, sodium chloride, agar, defibrinated sheep blood, phenylethyl alcohol, distilled water] (32), and Schleifer-Krämer (SK) agar [this medium has been used for selective isolation of *Staphylococcus* species and contains tryptone or peptone from casein, beef extract, yeast extract, glycerol, sodium pyruvate, glycine, KSCN, NaH_2PO_4 H_2O, Na_2HPO_4 $2H_2O$, LiCl, agar, and distilled H_2O] (4) and, tellurite glycine agar (containing tryptone, yeast extract, mannitol, K2HP04, lithium chloride, glycine, agar, potassium tellurite) (33). The incubation period for these specimens is at least 48 - 72 hours (4) at 37°C. Additionally, *S. argenteus* and *S. schweitzeri* were cultured on tryptone soy agar (TSA) (enzymatic digestions of casein and soybean meal, sodium chloride, and agar) at 37°C (34, 35). *Staphylococcus argenteus* has been isolated from community-acquired or healthcare-associated settings (36). Schutte *et al.* reported that *S. roterodami* could grow on BA, Brucella BA, chocolate BA, MacConkey agar without salt, and Muller-Hinton agar (14).

3. Food Specimens

Two species of this complex have been isolated from food products, including *S. aureus* (4, 39) and *S. argenteus* (32, 36, 40-42). Staphylococcal food poisoning and gastroenteritis may result from the consumption of food contaminated with enterotoxins (43). For isolation of these bacteria from food materials, non-selective enrichment of *S. aureus*, tryptic soy broth (TSB), and TSB containing 20% NaCl, Egg Yolk Tellurite enrichment, Trypticase soy broth with 10% NaCl and 1% sodium pyruvate (4), Baird-Parker agar (basal medium is containing agar, beef extract, glycine, lithium chloride $6H_2O$, tryptone, yeast extract) (4, 36), salt egg yolk (SEY) agar (41), and SK agar (basal medium containing agar, beef extract, distilled H_2O, glycine, glycerol, KSCN, LiCl, NaH_2PO_4 H_2O, Na_2HPO_4 $2H_2O$, tryptone or peptone from casein, sodium pyruvate, yeast extract) (4) have been recommended. The incubation period is set at 35 - 37°C for 24 - 48 hours.

4. Animal Specimens

Previous studies have reported the isolation of these bacteria from animals such as bats (44), bovine mastitis (45), gorillas (46, 47), pigs (47, 48), chickens (48), and rabbits (20) (*S. argenteus*). These studies have also reported infections in bats (44, 49, 50), gorillas (50), and monkeys (50, 51) (*S. schweitzeri*). Olatimehin *et al.* employed nutrient broth and Mannitol salt agar to isolate the *S. aureus* complex from fecal samples of Eidolon helvum at 37°C for 48 hours (44). In another

Table 1. Some Phenotypic Characterization of *Staphylococcus aureus* Complex

Variables	*Staphylococcus aureus*	*Staphylococcus argenteus* (MSHR1132^T)	*Staphylococcus schweitzeri*	*Staphylococcus singaporensis* (SS21^T)	*Staphylococcus roterodami*
Pigmentation	+	-1 [a]	+2 [b]		-
β-Hemolysis	+	+	+	+	+
Arginine Dihydrolase	+	+	+	+	+
Acetoin Production	+				
Alkaline Phosphatase	+	+	+	+	+
Catalase	+	+	+	+	+
Coagulase	+	+	+	+	+
Nitrate Reduction	+			+	+
Ornithine Decarboxylase	-			-	
L-Pyrrolidonyl Arylamidase	+	+	+		+
Urease	d [c]/-	-	-	+	-
Hydrolysis of Esculin	-				
Resistance to Novobiocin	-	-	-		-
Resistance to Polymixin B	+	+	+		+
β-Galactosidase	-	-	-		-
β-Glucosidase	+	-	-		
β-Glucuronidase	-	-	-		-
L-Arabinose	-				
D-Cellobiose	-				
Maltose	+	+	+	+	+
D-Mannitol	+	+	+	+	+
D-Mannose	+	+	+	+	+
Raffinose	-	-	-	-	-
D-Trehalose	+	+	+	+	+
Sucrose	+	+	+	+	+
D-Turanose	+				
D-Xylose	-	-	-	-	-
D-Glucose				+	
D-Fructose				+	
D-Galactose	+	+	-		+
Lactose	-	-	-	+	+
Growth in 6.5 % NaCl	+	+	+		+
Ref.	(4, 35)	(35)	(35, 37)	(38)	(14)

[a] Positive for 11 to 89% of strains.

[b] Creamy white appearance.

[c] Yellowish-pigmented, *nucA* gene was positive in all of species.

study by Schaumburg *et al.*, the *S. aureus* complex was isolated from animals and humans by culturing on Columbia BA plate, Columbia CAP selective agar (containing aztreonam and colistin) plate and SAID [*S. aureus* ID] agar plate for 18 - 36 hours at 36°C (51). Indrawattana et al. used sheep blood and Mannitol salt agar to isolate *S. argenteus* (at 37°C for 24 - 48 hours) (20).

5. Phenotypic Identification

Colonies suspected to be *Staphylococcus* should undergo gram staining and be identified at both the genus and species levels. Schutte *et al.* reported that *S. aureus* and *S. roterodami* exhibit similar Gram staining characteristics under microscopic examination (14). The color of *S. argenteus* colonies is silver, as this bacterium lacks the carotenoid pigment staphyloxanthin (52-54). Various phenotypic tests can differentiate staphylococci from other gram-positive cocci with catalase production. These tests include susceptibility to

Figure 1. Phylogenetic tree of *Staphylococcus* species based on 16S rRNA gene sequences, constructed using neighbor-joining (NJ) analysis and the Kimura 2-parameter (K2P) model the support of each branch was determined from 1000 bootstrap samples. Bar 0.02 substitutions per nucleotide position.

erythromycin and lysostaphin (55), bacitracin (56), furazolidone (57), growth in 6.5% NaCl, coagulase, nitrate reduction, urease, colony morphology, OF (oxidation-fermentation) test, oxidase, hydrolysis of Esculin, acid production from various carbohydrates such as arabinose, cellobiose, maltose, mannitol, mannose, raffinose, trehalose, sucrose, turanose, xylose, glucose, fructose, galactose, lactose, and others (58, 59). Staphylococci are non-motile, non-spore-forming bacteria; some species are facultative anaerobes, and

catalase and benzidine tests are positive in these species (4). *Staphylococcus roterodami*, *S. argenteus*, *S. schweitzeri*, and *S. singaporensis* test positive for coagulase enzymes, similar to *S. aureus* (14, 35, 38). They exhibit proximity to *S. aureus* when considering phenotypic and genotypic features (60). According to the phenotypic tests presented in Table 1, phenotypic identification alone is not entirely suitable for the *S. aureus* complex, and molecular methods are necessary for accurate identification at the species level. 16S rRNA gene sequence of *S. simiae* is similar to other members of the *S. aureus* complex (Figure 1), but some phenotypic test results such as coagulase, a-glucosidase, b-glucosidase, hydrolysis of DNA and esculin, and D-mannose were negative. However, acid production from D-maltose, D-mannitol, D-melezitose, D-trehalose, N-Acetylglucosamine, and resistance to polymyxin B were positive (61), indicating differences from these members. Conventional identification is inadequate for distinguishing four species in the *S. aureus* complex (38). To date, matrix-assisted laser desorption ionization-time of flight mass spectrometry (MALDI-TOF MS) has also been utilized for identifying the *S. aureus* complex (14, 20, 25, 35, 37, 44, 49, 62). Tong *et al.* compromised MALDI-TOF MS identity scores with two databases: A standard clinical database and an amended database with profile proteins from *S. aureus*, *S. argenteus*, and *S. schweitzeri*. In the standard/amended database, identity scores for *S. aureus*, *S. argenteus*, and *S. schweitzeri* were 2.295/2.295, 2.071/2.700, and 1.847/2.676, respectively (35). Indrawattana et al. used two methods, NRPS sequencing and MALDI TOF MS, to identify eight suspicious isolates of *S. argenteus*. The results of the two methods were reported to be similar (20). Another study by Chen *et al.* employed MALDI TOF MS for accurate differentiation between *S. aureus* and *S. argenteus*. They reported that this method correctly distinguished 100% of the 72 *S. argenteus* isolates from the 72 methicillin-susceptible *S. aureus* samples (25).

6. Molecular Identification

16S rRNA gene sequence analysis showed that this genus belongs to the phylum Firmicutes (59). DNA-DNA hybridization (4), 16S rRNA gene sequencing, and their comparative oligonucleotide (63) reveal genetic differences between the two genera *Staphylococcus* and *Micrococcus*. *Staphylococcus* is closely related to genera such as enterococci, *Lactobacilli*, *Listeria*, micrococci, and streptococci (4, 59). The DNA G+C content is 30 - 39 mol% in the *Staphylococcus* genus (4). More than 30 species of the genus *Staphylococcus*, especially *S. aureus*, *S. argenteus*, *S. schweitzeri*, *S. roterodami*, and *S. singaporensis* have been completely sequenced (https://www.ncbi.nlm.nih.gov/assembly/?term = *Staphylococcus*). Analysis of full-length 16S rRNA gene sequences showed that *S. argenteus*, *S. roterodami*, and *S. schweitzeri* have sequences that are closely related to *S. aureus* (14, 38). Additionally, these species exhibit differences in *nuc* gene nucleotides (37). Tong et al. reported the amplification of the *nuc* gene using conventional polymerase chain reaction (PCR) in *S. argenteus*, utilizing specific primers provided by Brakstad *et al.* (5'-GCGATTGATGGTGATACGGTI-3' forward and 5'-AGCCAAGCCTTGACGAACTAAAGC-3' reverse (64). They also reported the number of mismatches in the primer sites (35). Eshaghi *et al.* reported that 22 isolates of *S. argenteus* tested negative for *nuc* gene primers specific to *S. aureus* (37). Hansen *et al.* reported that the *nuc* length was 670 bp in all of the isolates of *S. argenteus*, whereas the *nuc* length was 687 bp in *S. aureus*. Additionally, they reported that the *S. argenteus nuc* gene homology was 83% with the *S. aureus nuc* gene (19). Another study by Zhang *et al.* reported that NRPS gene (*nrps*-F: 5'-TTGARWCGACATTACCAGT-3'/*nrps*-R: 5'-ATWRCRTACATYTCRTTATC-3') could simultaneously recognize and differentiate *S. argenteus* and *S. schweitzeri* from *S. aureus*, producing PCR products of ~340 base pairs and ~160 base pairs, respectively (36). Designing primers specific to *S. roterodami*, *S. argenteus*, *S. schweitzeri*, and *S. singaporensis* will be necessary for accurate and rapid identification. There are various methods for bacterial whole-genome sequencing (WGS), including massively parallel sequencing, Sanger sequencing, and single-molecule sequencing (65, 66). There are various sequencing platforms, including Illumina, MiSeq, MiniSeq, NextSeq, NovaSeq, Ion Torrent, S5, Pyrosequencing, Pacific Biosciences, and Oxford Nanopore sequencing techniques (66-68). To date, WGS is a reliable tool for the taxonomic description of bacterial species, epidemiological studies, and clinical data (69, 70). Based on complete genome sequencing, we can generate a phylogenomic tree and assess the position of species on the evolutionary tree. Also, we can compare two or more species with DNA-DNA hybridization and average nucleotide identity by blast (ANIb) based on the genomic sequences (71). The

standard cut-off for ANIb is generally set at 95 - 96% (72, 73). Comparisons based on the whole-genome of *S. argenteus* (MSHR1132^T) and *S. schweitzeri* (DSM 28300^T) to *S. aureus* demonstrate significant phylogenetic differences, with an average nucleotide identity (ANI) value and DNA–DNA hybridization (dDDH) of 95% and 70% respectively (35). Average nucleotide identity by blast between *S. argenteus* MSHR1132 ^{T} and *S. schweitzeri* DSM 28300 ^{T} was 92.03%, below the species delineation cut-off. Suzuki *et al.* conducted a comparative genomic analysis and reported that *S. simiae* is the sister taxon of *S. aureus* (74). The ANIb and the percentage of aligned nucleotides [%] for the whole genome sequences of two members of the *S. aureus* complex are shown in Table 2. The last study reported that multilocus sequence typing (MLST) is a powerful tool for identifying *S. argenteus*.

7. Multilocus Sequence Typing

Multilocus sequence typing is a method that generally involves the amplification of seven housekeeping gene loci using PCR. In the following, PCR products are sequenced, and then these nucleotide sequences are compared to established allelic profiles. A variation in a single nucleotide at any loci showed a distinct allele, contributing to determining the sequence type (ST) (75). Zhang *et al.* reported three new STs, including ST3261, ST3262, and ST3267 (36). In the literature, for the taxonomy of the genus *Staphylococcus*, five housekeeping genes, namely *gap*, *hsp60*, *rpoB*, *sodA*, and *tuf*, have been used and are suitable for distinguishing *S. argenteus* from *S. aureus* (76). Wu *et al. utilized* the MLST method with several housekeeping genes such as *arcC*, *aroE*, *glpF*, *gmk*, *pta*, *tpi*, and *yqil* to identify *S. argenteus*. In their study, eight different STs were identified in the 114 isolates, and they reported five new types, including ST5054, ST5055, ST5056, ST5057, and ST5058. ST2250 was the most common ST, and the prevalence of ST1223, ST2854, ST5057, ST5054, ST5056, ST5058, ST5055 were 14.0%, 2.6%, 2.6%,1.8%,1.8%,1.8%,0.9% respectively. They reported two clonal complexes, including CC2250 and CC1223 (42). Indrawattana *et al.* reported STs in the *Staphylococcus* complex, including ST4209, ST4210, ST4211, ST4212, and ST4213 (20). Hsu *et al.* performed MLST on 96 isolates of *S. argenteus*, and they reported four STs: ST1223 (10.4%), ST2198 (2.1%), ST2250 (75%), and ST2793 (12.5%). In their study, all ST2250 isolates harbored CRISPR loci, while other types did not carry CRISPR loci. They also employed pulsed-field gel electrophoresis (PFGE) and *Spa* typing for genetic associations. Other genes, including *Coa*, *DnaJ* (hsp40), *GroEL* (hsp60), spacer sequencing, and accessory gene regulator (*agr*) group have been sequenced and analyzed (62). The phylogenetic tree of the *Staphylococcus* species was constructed using the molecular evolutionary genetics analysis program version 5 (MEGA5) (Figure 1).

8. Clinical Diseases, Virulence Factors, Antibiotic Resistance, and Epidemiology

Staphylococcus argenteus infections caused by *S. argenteus* are associated with various clinical manifestations, with a higher prevalence in skin and soft tissue infections. Compared to *S. aureus*, this bacterium is more sensitive to oxidative stress and susceptible to neutrophil killing due to the lack of pigment staphyloxanthin and fewer virulence factors (4, 77, 78). Human infections with *S. argenteus* are linked to a milder course of the disease (12, 79). Compared with *S. aureus*, *S. argenteus* infections cause less respiratory failure during hospitalization, with a non-significant similar trend for shock and no difference in mortality within 28 days. *S. argenteus* is also more susceptible to antimicrobial drugs (24). Although it can induce blood infection (24, 79, 80), bacteremia associated with *S. argenteus* poses a higher risk of mortality than methicillin-sensitive *S. aureus* (MSSA) associated with bacteremia (81). Additionally, it may lead to nosocomial infections and invasive diseases (25, 79). *Staphylococcus argenteus* has been isolated from the blood culture of a woman with necrotizing fasciitis infection in Australia (52). This bacterium (22WJ8192) was isolated from a blood sample taken from the peripheral vein of a seven-month-old female infant in Eastern China (29). On the other hand, *S. argenteus* infection is more likely to lead to kidney disease and diabetes in adults than MSSA (79). It causes various infections such as mycotic aortic aneurysm (82), bone and prosthetic joint infection (83-85), purulent lymphadenitis (86), foreign-body infections (87), atopic dermatitis lesions (88), and keratoconjunctivitis (89). Although this group of bacteria may be pathogenic in food and milk, it may also trigger bovine mastitis (90). Small colony variants (SCVs) of *S. argenteus* strain pose challenges to therapeutic strategies, especially when amikacin is used or in chronic infections (91). *Staphylococcus argenteus* carries several toxin genes, such as Panton-Valentine leukocidin (20, 41, 47, 77, 80, 92-94). However, some

Table 2. Average Nucleotide Identity by Blast and (Aligned Nucleutides) [%] of Whole Genome Sequences of Four Members of *Staphylococcus aureus* Complex [a]

Organism	*Staphylococcus argenteus* MSHR1132 [T]	*Staphylococcus aureus* 502A	*Staphylococcus roterodami* Zoo-28	*Staphylococcus schweitzeri* DSM 28300 [T]
***S. argenteus* MSHR1132** [T]	-	87.62 (84.55)	93.47 (87.04)	92.03(86.41)
***S. aureus* 502A**	87.41 (85.98)	-	87.85 (84.39)	88.69 (86.05)
***S. roterodami* Zoo-28**	92.82 (87.55)	87.81 (81.67)	-	92.74 (85.00)
***S. schweitzeri* NCTC13712** [T]	91.82 (87.40)	88.72 (86.13)	92.83 (86.83)	-

[a] Genome sequence of type strain *S. singaporensis* was not available in Genebank database.

findings have indicated a lower prevalence of virulence genes than *S. aureus* (77, 93). Other findings suggest the absence of the *pvl* virulence gene in it (24, 95-98).

Recently, whole genome sequencing (WGS) revealed that the nucleotide sequence similarity in the *pvl* gene between *S. argenteus* and *S. aureus* is 75%, and this gene is more prevalent among *S. argenteus* isolates (94). *Staphylococcus argenteus* contains the *esxB* to induce pathogenesis of abscess; the ear gene is proposed for penicillin-binding protein and, *ebh*, *esaB*, *seh*, *chp*, *lip*, *seg*, *esaC*, *esxB*, *sei*, *selu2*, *selm*, and *selo* as adherence genes (19). Furthermore, other virulence factors such as *atlE* (autolysin), *ebp* (elastin binding protein), (37), *icaA*, *icaB*, *icaC*, and *icaR*, *clfA*, *clfB*, *fnbA*, *fnbB*, *fib*, and *cna* (intercellular adhesion) (37, 42, 84), *sak* (staphylokinase) (19, 21, 37, 47, 85, 99-101), *scn* (staphylococcal complement inhibitor) (19, 37, 47, 85, 101), *spa* (staphylococcal protein A) (37, 38), *sspB* (cysteine protease), *hysA* (hyaluronate lyase) (37), *geh* and lip (lipase) (19, 37), *coa* (staphylocoagulase) (37, 38, 99), *nuc* (thermonuclease) (37), *cap5* and *cap8* (capsular) (19, 37), *hla* (alpha hemolysin) (20, 37, 41, 77, 93, 94, 99), *hld* (delta hemolysin) (37), *eta* (exfoliative toxin type A) (37, 99) and *hlgA*, *hlgB*, and *hlgC* (gamma hemolysin) (37, 99), *tst* (toxic shock syndrome toxin) (19-21, 23, 37, 41, 47, 77, 92-94, 99, 101, 102), *esaC*, *esxB*, *esxA*, *esaG*, *essA*, *essB*, *essC*, *adsA*, and *essA* (type VII secretion system) (19, 47), *mazE*, *Yef M* [antitoxin component of type-II toxin-antitoxin (TA) system] (47), *can* (collagen binding protein), *bap*, and *eno* (biofilm production genes) (42), *bbp* (sialoprotein-binding protein gene) (62) have been reported in this group of bacteria. It forms silver colonies due to the lack of production of the carotenoid pigment staphyloxanthine, encoded by the operon crtOPQMN. Carotenoid pigment expression is associated with decreased bacterial virulence and density in the cardiac valve, spleen, and kidneys (53). The rate of antibiotic resistance appears to be lower in the members of the genus of *S. aureus* complex than in *S. aureus* (24). *Staphylococcus argenteus* strains seem to acquire more antibiotic resistance genes (Table 3) than other species (*S. schweitzeri*, *S. singaporensis*, and *S. roterodami*), especially in clinical isolates, and it is an issue of concern (103). While the isolates of penicillin-resistant (with or without *blaZ*) strains are common (20, 21, 23, 99-101), other antibacterial resistance are scarce, such as tetracycline (with or without *tet* genes), gentamycin, clindamycin, erythromycin, fusidic acid, ampicillin, and daptomycin (18, 41, 42, 99, 100, 104). Regarding the prevalence of methicillin resistance isolates (cefoxitin or oxacillin with or without *mecA* genes), findings vary across the globe (19, 37, 101, 103, 104). Nevertheless, the presence of *SCCmec* type IV is rarely indicated (19, 94, 101). In numerous epidemiological studies, *S. argenteus* is associated with various human and animal specimens. It has been reported from Southeast Asian countries, including Thailand (4 studies), Japan (6 studies), Myanmar, Taiwan, China (2 reports each), and Singapore (1 study). Relatively few studies have been reported from African and European countries, including Sweden (2 studies), Gabon, Nigeria, Denmark, France, Belgium (each country with one report), and England (2 studies), However, recent efforts have shown an increased focus on these regions (Table 4).

Staphylococcus schweitzeri: *S. schweitzeri* is typically acquired as a strain that colonizes the nasopharynx of Afrotropical wildlife, particularly in primates and bats. However, it can also be found on fomites (50, 51, 106), and three *S. schweitzeri* isolates have been reported from human nasopharyngeal samples in Gabon (107). It has exhibited nearly the same virulence factor as those presented in other *S. aureus* complexes, such as exfoliative toxins, toxic shock syndrome toxin (*tst*)

Table 3. Antibiotic Resistance Profiles of *Staphylococcus* Species

Bacterium	Common Resistant Antibiotics	Common Susceptible Antibiotics	Resistance Genes
Staphylococcus argenteus	Penicillin (with/without *blaZ*), tetracycline (with/without *tet* genes), gentamicin, clindamycin, erythromycin, fusidic acid, ampicillin, daptomycin	More susceptible than *S. aureus*; lower antibiotic resistance overall	*mecA* (variable prevalence), *SCCmec* type IV (rare), *blaZ*, *tet* genes
S. schweitzeri	No reported resistance	Susceptible to all tested antibiotics	No known resistance genes
S. singaporensis	One isolate resistant to gentamicin	Susceptible to penicillin, mupirocin, oxacillin, erythromycin, clindamycin, fusidic acid, ciprofloxacin, minocycline, linezolid, trimethoprim-sulfamethoxazole, teicoplanin, quinupristin-dalfopristin, vancomycin	No known resistance genes
S. roterodami	Resistant to polymyxin B	Susceptible to cefoxitin, benzylpenicillin, oxacillin, gentamicin, tobramycin, ciprofloxacin, levofloxacin, erythromycin, clindamycin, linezolid, teicoplanin, vancomycin, tetracycline, fosfomycin, nitrofurantoin, fusidic acid, mupirocin, rifampicin, trimethoprim-sulfamethoxazole	No known resistance genes

enterotoxins (*seb*, *sec*), Panton-Valentine leukocidins (50, 51), autolysins, hemolysins (*hla*) (49, 50), adhesins, polysaccharide capsules, immune evasion factors, and fibronectin-binding proteins (FnBPA, FnBPB) (50, 51). It can exert a cytotoxic effect on the human cell line (77) and has demonstrated host cell invasion, activation of host cells with the induction of pro-inflammatory cytokines, and intracellular cytotoxicity comparable to *S. aureus*. However, its extracellular cytotoxicity surpasses that of *S. aureus*. Moreover, it can produce more biofilm than *S. aureus* but is lower than *Staphylococcus* epidermidis. It is also capable of escaping from phagolysosomes (50). However, fecal specimens from straw-colored fruit bats (Eidolon helvum) (44) and fomites *S. schweitzeri* isolates revealed the absence of virulence and antibiotic resistance genes. Only one of the isolates contains *icaC* (intracellular adhesion gene) (106). Seems likely *S. schweitzeri* will emerge as a zoonotic strain within the genus *Staphylococcus*. As of now, no antibiotic resistance has been reported (107). In terms of epidemiology, *S. schweitzeri* appears to be associated with wildlife. It has been reported in several countries, including Gabon (2 reports), Nigeria (2 reports), Côte d'Ivoire, and Congo (1 report).

9. *Staphylococcus singaporensis* and *Staphylococcus roterodami*

The clinical manifestations of *S. singaporensis* isolated from cholecystostomy were similar to those caused by *S. aureus*. It led to skin and soft tissue infections in 66.7% of cases. However, *S. singaporensis* appears to possess fewer toxin genes than *S. aureus*. This bacterial group contains staphylococcal protein A, coagulase, and *crtM* genes, but it lacks staphylococcal enterotoxins, *tst-1*, *pvl*, and mobile genetic elements such as phages, pathogenicity islands, and genomic islands (38). *Staphylococcus roterodami* has been isolated from a foot wound specimen in the Erasmus Medical Center in Rotterdam. However, this bacterium's pathogenicity and virulence factors have not been investigated (14). Overall, *S. singaporensis* isolates are susceptible to various antibiotics, including penicillin, mupirocin, oxacillin, erythromycin, clindamycin, fusidic acid, ciprofloxacin, minocycline, linezolid, trimethoprim-sulphamethoxazole, teicoplanin, quinupristin – dalfopristin, and vancomycin while one isolate shows resistance to gentamicin (38). On the other hand, *S. roterodami* is susceptible to all antimicrobial drugs, including cefoxitin, benzylpenicillin, oxacillin, gentamycin, tobramycin, ciprofloxacin, levofloxacin, erythromycin, clindamycin, linezolid, teicoplanin, vancomycin, tetracycline, fosfomycin, nitrofurantoin, fusidic acid, mupirocin, rifampicin, trimethoprim-sulfamethoxazole, except for polymyxin B (14). *S. singaporensis* and *S. roterodami* differ in their epidemiology; *S. singaporensis* has been reported from Singapore, while *S. roterodami* has been indicated from Indonesia. As of this writing, no further reports of these bacteria have been published, and no data on resistance genes, virulence factors, and the epidemiology of these bacteria are available.

10. Role of *Staphylococcus aureus* Complex in Food Poisoning

Staphylococcal food poisoning (SFP) is caused by staphylococcal enterotoxins (*SEs*), which are formed beforehand in food products. Various species of Staphylococci, including *S. aureus* and recently *S. argenteus*, carry *SE* genes found in mobile genetic elements (41, 109). Different studies have proposed

twenty *SE* and SE-like genes, including five classical enterotoxins (*sea*-to-*see* genes) (110, 111). Various new *SEs* (*SEG*, *SEH*, *SEI*, *SEM*, *SEN*, and *SEO*) have recently been identified as triggers for SFP without producing *SEs* (112, 113). As mentioned, *S. argenteus* is also one of the leading causes of foodborne diseases globally, with various staphylococcal enterotoxin genes (*sea*, *sec*, *sed*, *seb*, *seg*, *sei*, *sem*, *sen*, *seo*, *selu2*, *sec3*, *ear*, *selk*, *selq*, *selX*, *secY*, *sey*, *sea*, *sed*) reported from food specimens (19-21, 23, 41), (37, 47, 77, 92-94), (99, 101, 102).

11. Conclusions

The present review focuses on the unique clinical, taxonomic, and antimicrobial resistance profiles of the *S. aureus* complex, specifically *S. argenteus*, *S. schweitzeri*, *S. roterodami*, and *S. singaporensis*. Although *S. argenteus* and *S. aureus* share similarities, *S. argenteus* has a lower virulence but a higher bacteremia-related mortality. *S. schweitzeri* is mainly linked to wildlife and has the potential to be transmitted to humans, while *S. singaporensis* and *S. roterodami* remain poorly understood. Significant knowledge gaps in global epidemiology, resistance mechanisms, and transmission patterns need further genomic and clinical research. Accurate diagnosis, infection control, and food safety monitoring are crucial to minimize these emerging pathogens' risks.

Footnotes

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Table 4. Characteristics of the Studies Included in the Review of *Staphylococcus aureus* Complex

Country	Year	Type of Study	Sample Type	Total Sample	Values	Identification Method			Bacteria Species	Ref.
						Sequence-based/ Conventional PCR Methods	Band-based Methods	MALDI-TOF		
Thailand	2016	Prospective cohort observational study	Sepsis (abscesses n = 163, blood n = 115, bone or arthocentesis n = 21, body fluids, biliary tract and cerbrospinal fluid n = 7, pus from implanted surgical hardware n = 3, pus from spaces such as sinuses and inner ear n = 2)	311	58 (19)	MLST	PFGE		*S. argenteus*	(24)
Japan	2017	Case study	Fecal specimens, food, table, workbench, and empty lunch boxes	10	10	WGS, MLST			*S. argenteus*	(40)
Japan	2018	2 case study	Fecal specimens, food samples, and swabs of cooking utensils	51	36	MLST	PFGE		*S. argenteus*	(40)
Gabon	2016	Research article	Faucal specimens of wild-living apes (gorilla)	1	-	MLST		MALDI-TOF MS	*S. argenteus*	(46)
Japan	2020	Retrospective observational cohort study	Blood culture	21	2 (1)	MLST			*S. argenteus*	(23)
Thailand	2015	Cohort	Invasive infection (Blood culture)	246	10 (4.1)	MLST			*S. argenteus*	(18)
Myanmar	2017		Nasal swab (food handlers)	563	5 (4.5) (in 110 carrier)	MLST			*S. argenteus*	(105)
Taiwan	2018	Retrospective study	Blood culture	915	97	MLST		MALDI-TOF MS	*S. argenteus*	(25)
Thailand	2019	Original article	Pus (rabbits)	67 (19 bacteria isolates)	3	MLST		MALDI-TOF MS.	*S. argenteus*	(20)
Gabon	2021	An in vitro study	Monkeys (n = 38), bats (n = 16), humans (n = 3) and gorilla (n = 1)	156	58	MLST, WGS			*S. schweitzeri*	(50)
Nigeria	2020		Fomites samples (currency note, computer keyboard)	239	2	MLST, Wholegenome sequencing		MALDI-TOF MS	*S. schweitzeri*	(106)
Nigeria	2018	Original article	Fecal samples from E. helvum	250 samples (53 isolates)	11 (14)	MLST		MALDI-TOF MS	*S. schweitzeri*, *S. argenteus*	(44)
Gabon	2017	Short communication	Pharyngeal swabs (Bat)	133	2 (4)	PCR, MLST		MALDI-TOF MS	*S. schweitzeri*	(49)
Côte d'Ivoire, Gabon, Congo	2014	Cross-sectional study	Anterior nares and the pharyngeal mucosa (human and monkey)	Human (1288) and animal (698)	24	PCR, MLST			*S. schweitzeri*	(51)
United Kingdom	2021	Molecular epidemiology case-study	Nasal and throat swab RM recruits)	1012	6 (4 recruits)	WGS, MLST			*S. argenteus*	(99)
Japan	2019		Clinical specimens: Sputum (6), pharyn× (2), nasal discharge (2), stool (4), skin and abscess (3), urine (2), vaginal discharge (2), ear discharge (1), blood (1), and subdural abscess (1)	23 patients	24	PCR, MLST		MALDI-TOF MS	*S. argenteus*	(21)
Thailand	2017		Invasive infection		68	WGS, MLST, PCR			*S. argenteus*	(100)
Denmark	2017		Skin and soft tissue infection, wounds, the ear, the nose		25	WGS, MLS, PCR			*S. argenteus*	(19)
Sweden	2019		Throat swab, perineum, wound, abces, eczema		16	WGS	PFGE	MALDI-TOF MS	*S. argenteus*	(104)
Belgium	2016	Retrospectively study	Clinical laboratories, nasal samples	1650	3 (0.16)	MLST and *SCCmec* typing			*S. argenteus*	(101)
China	2016	Short communication	Food products, healthy humans, or hospital infections	839	6	MLST			*S. argenteus*	(36)
United Kingdom	2021	Original article	Human, Pig, Gorilla		132	MLST, CRISPRCasFinder web-server			*S. argenteus*	(47)
France	2020	Case study	Prosthetic-joint infection		1	WGS			*S. argenteus*	(84)

Country	Year	Type of Study	Sample Type	Total Sample	Values	Identification Method			Bacteria Species	Ref.
						Sequence-based/ Conventional PCR Methods	Band-based Methods	MALDI-TOF		
Sweden	2020	Short Research Communication	Prosthetic-joint infection		1	WGS		MALDI-TOF MS	*S. argenteus*	(87)
North American	2021	Original article	Clinical samples (sterile sites, 11 from nonsterile sites, and 4 from surveillance screens)		22	WGS, 16S rRNA gene analysis		MALDI-TOF MS	*S. argenteus*	(37)
Singapore	2021	Retrospective cohort study	Clinical and screening samples	43	37	WGS, MLST			*S. argenteus*,	(38)
Singapore	2021	Retrospective cohort study	Clinical and screening samples	43	6	WGS, MLST			*S. singaporensis* sp.	(38)
Indonesia	2021		Foot wound		1	16S phylogeny, MLST		MALDI-TOF MS	*S. roterodami* sp.	(14)
Gabon	2016	Cross-sectional study	Human throat swabs, skin lesions	103	3 (2 from school children)	MLST			*S. schweitzeri*	(107)
China	2020		Retail foods (4300 samples)	1581	114	MLST			*S. argenteus*	(42)
United States	2020	Case report	Hemodialysis catheter		1			MALDITOF MS	*S. argenteus*	(18)
Taiwan	2020		Blood		96	MLST	PFGE	MALDI-TOF MS	*S. argenteus*	(26)
Myanmar	2019	Research article	Nasal isolates of healthy food handlers (563), clinical isolates (wound swab, pus, and blood)	144 + 137	6	MLST			*S. argenteus*	(108)
Japan	2020	Case report	Conjunctival scraping		1	Whole-genome sequence, MLST		MALDITOF MS	*S. argenteus*	(89)
Japan	2021		Clinical specimens	82	3 (0.66)			MALDI-TOF MS	*S. argenteus*	(103)

Abbreviations: RM, royal marines; WGS, whole-genome sequencing; PCR, polymerase chain reaction; MLST, multilocus sequence typing.