Novel staphylococcal species that form part of a Staphylococcus aureus-related complex: the non-pigmented Staphylococcus argenteus sp. nov. and the non-human primate-associated Staphylococcus schweitzeri sp. nov.

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We define two novel species of the genus Staphylococcus that are phenotypically similar to and have near identical 16S rRNA gene sequences to Staphylococcus aureus. However, compared to S. aureus and each other, the two species, Staphylococcus argenteus sp. nov. (type strain MSHR1132T = DSM 28299T = SSI 89.005T) and Staphylococcus schweitzeri sp. nov. (type strain FSA084T = DSM 28300T = SSI 89.004T), demonstrate: 1) at a whole-genome level considerable phylogenetic distance, lack of admixture, average nucleotide identity 95 %, and inferred DNA–DNA hybridization 70 %; 2) different profiles as determined by MALDI-TOF MS; 3) a non-pigmented phenotype for S. argenteus sp. nov.; 4) S. schweitzeri sp. nov. is not detected by standard nucA PCR; 5) distinct peptidoglycan types compared to S. aureus; 6) a separate ecological niche for S. schweitzeri sp. nov.; and 7) a distinct clinical disease profile for S. argenteus sp. nov. compared to S. aureus.

There are over 40 species of the genus Staphylococcus, of which the coagulase-positive Staphylococcus aureus is a major cause of human clinical disease. The population structure of S. aureus is well-understood and comprises clonal complexes (CCs) with <2 % nucleotide divergence. Recently two Staphylococcus lineages have been recovered from human clinical infections (Holt et al., 2011; Ng et al., 2009; Ruimy et al., 2010; Tong et al., 2010), from non-human primates (Schaumburg et al., 2012), and from bats in Africa (Akobi et al., 2012). These lineages have previously been identified...
been identified as *S. aureus* according to phenotype, but on the basis of multi-locus sequence typing (MLST) and a single genome sequence, the lineages are allied to but significantly diverged from *S. aureus*. We describe here investigations including the use of whole-genome sequence analysis to justify classification as three separate species, *S. aureus*, and two novel species of the genus *Staphylococcus*. Strain MSHR1132<sup>T</sup> was isolated from blood cultures of an Indigenous patient from Darwin, Australia (Holt et al., 2011); and strain FSA084<sup>T</sup> was isolated from the nares of a red-tailed monkey (*Cercopithecus ascanius*) from Gabon, Africa (Schaumburg et al., 2012). Both strains grew on tryptone soy agar (TSA) at 37 °C with large, round, smooth colonies similar to typical *S. aureus*. Colonies of FSA084<sup>T</sup>
have a yellowish-pigmented appearance while those of MSHR1132\textsuperscript{T} are non-pigmented, displaying a creamy white appearance. The difference in pigmentation between typical \textit{S. aureus} and strain MSHR1132\textsuperscript{T} is particularly evident after growing on chocolate agar (Oxoid) for 48 h at 37°C (Holt \textit{et al.}, 2011). Strains MSHR1132\textsuperscript{T} and FSA084\textsuperscript{T} are both catalase-positive, coagulase-positive by tube coagulase test and colonies demonstrate \(\beta\)-haemolysis on blood agar. Gram staining tests revealed Gram-stain-positive cocci in clusters for both strains. MLST revealed MSHR1132\textsuperscript{T} as ST1850 and FSA084\textsuperscript{T} as ST2022. We also selected for further investigation five strains that clustered according to MLST with MSHR1132\textsuperscript{T} (LBSA043, JABA32044, M260, M051, H115100079) and five that clustered with FSA084\textsuperscript{T} (FSCB1B, FSCB5, FSA096, FSA090, FSA037). The MSHR1132\textsuperscript{T} lineage strains were all recovered from human hosts from northern Australia (Brennan \textit{et al.}, 2013; McDonald \textit{et al.}, 2006), Fiji (Jenney \textit{et al.}, 2014) and the UK. The FSA084\textsuperscript{T} lineage strains were recovered from non-human primates in Gabon and Côte d’Ivoire, Africa (Schaumburg \textit{et al.}, 2012). These additional strains demonstrated the same cell and colonial morphology as MSHR1132\textsuperscript{T} and FSA084\textsuperscript{T} respectively. All MSHR1132\textsuperscript{T} lineage strains appeared non-pigmented.

Whole-genome sequencing using the Illumina HiSeq platform of the 12 strains, followed by core-genome single nucleotide polymorphism (SNP)-based maximum-likelihood trees demonstrated that MSHR1132\textsuperscript{T} lineage strains, FSA084\textsuperscript{T} lineage strains, and reference \textit{S. aureus} genomes, form three distinct clusters with 100% bootstrap support (Fig. 1). The details and GenBank accession numbers for these strains are provided in Table 1. Compared to \textit{S. aureus}, the 16S rRNA gene sequence (1474 nt) is identical in strain MSHR1132\textsuperscript{T} and differs at one position in strain FSA084\textsuperscript{T}. However, pairwise average nucleotide identity (ANI), as calculated using JSpecies (Richter & Rossello-Móra, 2009), across the genomes within and between these

### Table 1. Strains and GenBank accession numbers for whole-genome sequences

| Strain                        | Place of origin | GenBank accession nos of whole-genome sequences |
|-------------------------------|-----------------|-------------------------------------------------|
| \textit{Staphylococcus argenteus} sp. nov. JABA32044V6S1 | Fiji            | ERS140248 CCE01000001–CCE01000018 |
| LBSA043                       | Northern Australia | ERS140026 CCEM01000001–CCEM01000011 |
| M051                          | Northern Australia | ERS140254 CCEN01000001–CCEN01000011 |
| M260                          | Northern Australia | ERS140095 CCEF01000001–CCEF01000019 |
| H115100079                    | UK              | ERS154949 CCEP01000001–CCEP01000012 |
| MSHR1132\textsuperscript{T}   | Northern Australia | ERS821777 |
| \textit{Staphylococcus schweitzeri} sp. nov. FSA037 | Gabon           | ERS140147 CCEH01000001–CCEH01000058 |
| FSA084\textsuperscript{T}     | Gabon           | ERS140266 CCEL01000001–CCEL01000035 |
| FSA090                        | Gabon           | ERS140239 CCEO01000001–CCEO01000035 |
| FSA096                        | Gabon           | ERS140159 CCEK01000001–CCEK01000047 |
| FSCB1B                        | Côte d’Ivoire   | ERS140162 CCEG01000001–CCEG01000026 |
| FSCB5                         | Côte d’Ivoire   | ERS140167 CCEQ01000001–CCEQ01000038 |

\textit{Staphylococcus aureus} DSM 20231\textsuperscript{T} AMYL01000000 JH1 CP000736 RF122 AJ938182 ST398 AM990992 MSSA476 BX571857 JKD6159 CP002114 TW20 FN433596
Table 2. Genome-wide average nucleotide identities (ANI) and inferred DNA–DNA hybridization (DDH) values for pairwise comparisons of strains from each of the three groups

Values are mean with standard deviation. ANI was calculated using JSpecies (Goris et al., 2007) and inferred DDH with Genome BLAST Distance Phylogeny (Meier-Kolthoff et al., 2013).

| Group                        | ANI (95 % CI) | Pairwise comparison with: |
|------------------------------|--------------|----------------------------|
|                              | 1            | 2            | 3            |
| 1. S. argenteus sp. nov.     | 98.8 (0.14)  | 92.0 (0.08)  | 87.4 (0.20)  |
| 2. S. schweitzeri sp. nov.   | 89.1 (1.37)  | 46.4 (0.16)  | 33.5 (0.37)  |
| 3. S. aureus                 | 98.0 (0.44)  | 88.6 (0.14)  | 36.3 (0.23)  |

groups was consistent with separate species designations (Table 2). Previously it has been demonstrated that an ANI <95% corresponds well to a DNA–DNA hybridization (DDH) value of <70% (Goris et al., 2007). Similarly, an analysis using the Genome BLAST Distance Phylogeny (Meier-Kolthoff et al., 2013) to calculate genome-to-genome distances clearly demonstrated three separate groups with mean inferred DDH values of 34% and 36% between S. aureus and the MSHR1132T and FSA084T lineages, respectively, 46% between MSHR1132T and FSA084T lineages, and >80% within lineages (Table 3). An analysis of orthologous core genes shared by all three groups using Bayesian Analysis of Population Structure (BAPS) software (Cheng et al., 2013) demonstrated three BAPS clusters and an absence of admixture between the groups (Fig. 1). All MSHR1132T lineage strains lacked the carotenoid pigment operon.

PCR amplification of the nucA gene that is used as a standard confirmatory marker for S. aureus is positive in strain MSHR1132T but negative in strain FSA084T. An examination of the nucA gene and in particular the primer sites for nucA (Brakstad et al., 1992) reveal one and two mismatches for the forward primer, and five and five mismatches for the reverse primer, for MSHR1132T and FSA084T, respectively (Fig. 2). The presence of mismatches at the 3’ end of primers for strain FSA084T most likely contributes to the lack of amplification of product for strain FSA084T. There were two in-frame deletions of 9 and 12 bp and one in-frame insertion of 3 bp in both MSHR1132T and FSA084T nucA sequences compared to S. aureus.

Biochemical profiling was performed with the Vitek2 GP card platform (bioMérieux) according to the manufacturer’s instructions. We tested in triplicate each of the 12 strains together with 18 strains of S. aureus from the ATCC collection (ATCC 12600T, 13565, 13709, 14458, 19095, 19636, 23235, 25904, 25923, 27664, 29213, 29247, 33591, 33592, 43300, 49230, 49775, 51811) (Table 3). The biochemical test profiles for both MSHR1132T lineage strains and FSA084T lineage strains, are consistent with S. aureus, with mean probabilities of >95% of identity as S. aureus. Although no test definitively discriminated between the three groups, the following may be helpful in identifying these lineages. The FSA084T lineage strains were positive for D-ribose in 72% of tests compared to 4% and 17% for S. aureus and MSHR1132T lineage strains.

Table 3. Key biochemical tests used for identification of staphylococcal species

Species: 1. S. aureus [number of strains (n)=18]; 2, S. schweitzeri sp. nov. (n=6); 3, S. argenteus sp. nov. (n=6). Results were obtained in triplicate for each of MSHR1132T lineage (S. argenteus sp. nov.) strains, FSA084T lineage (S. schweitzeri sp. nov.) strains, and 18 ATCC strains of S. aureus using a Vitek2 GP Card (bioMérieux); see text for details of strains. Values are the proportion (%) of tests that were either positive or negative for each group of strains.

| Biochemical test           | 1       | 2       | 3       |
|----------------------------|---------|---------|---------|
| D-Xylose                   | –       | (100)   | (100)   |
| Arginine dihydrolase 1     | +       | (100)   | (100)   |
| β-Galactosidase            | –       | (96)    | (100)   |
| Phosphatase                | +       | (100)   | (100)   |
| β-Glucuronidase            | –       | (100)   | (100)   |
| L-Pyrroloidanyl arylamidase| +       | (100)   | (94)    |
| Urease                     | –       | (100)   | (100)   |
| Polymyxin B resistance     | +       | (94)    | (100)   |
| Lactose                    | –       | (97)    | (100)   |
| N-Acetyl-D-glucosamine     | +       | (98)    | (67)    |
| Maltose                    | +       | (100)   | (100)   |
| Novobiocin resistance      | –       | (98)    | (67)    |
| Growth in 6.5% NaCl        | +       | (100)   | (100)   |
| D-Mannitol                 | +       | (100)   | (100)   |
| D-Mannose                  | +       | (100)   | (100)   |
| Raffinose                  | –       | (100)   | (100)   |
| Sucrose                    | +       | (100)   | (100)   |
| Trehalose                  | +       | (83)    | (100)   |
| D-Ribose                   | –       | (96)    | (72)    |
| D-Galactose                | +       | (82)    | (56)    |
Two novel staphylococcal species related to S. aureus

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respectively. The MSHR1132\textsuperscript{T} lineage strains were positive for urease in 56\% of tests compared to 0\% for both S. aureus and FSA084\textsuperscript{T} lineage strains. S. aureus was positive for N-acetyl-D-glucosamine in 98\% of tests compared to 33\% and 28\% for FSA084\textsuperscript{T} lineage strains and MSHR1132\textsuperscript{T} lineage strains, respectively.

We attempted to discriminate 12 MSHR1132\textsuperscript{T} lineage strains (an additional six strains to those already described), 12 FSA084\textsuperscript{T} lineage strains (an additional six strains to those already described), and 22 consecutive standard clinical strains of S. aureus by using matrix-assisted laser desorption ionization–time of flight mass spectrometry (MALDI-TOF MS) (Microflex LT MALDI-TOF instrument; Bruker Daltonik) (Table 4). We prepared samples using liquid phase formic acid extraction, according to the manufacturer’s recommendations, and compared the spectral profiles gained to the existing Bruker standard clinical database of profiles using MALDI Biotyper 2.1 software (Bruker Daltonik) with default settings. Strains of S. aureus were confidently identified. The MSHR1132\textsuperscript{T} lineage strains and FSA084\textsuperscript{T} lineage strains profiles were most similar to the S. aureus profile, but identity scores were much lower than for the strains of S. aureus (P<0.0001 for both compared to S. aureus) and fell below the manufacturer’s recommended threshold for a species level identification. We generated new reference profiles with three MSHR1132\textsuperscript{T} lineage strains and three FSA084\textsuperscript{T} lineage strains and repeated the analysis of all 46 strains. All strains were then confidently identified into their different groups. These findings are consistent with the three groups being separate species based on cell proteomic analysis.

Analyses of fatty acids, respiratory quinones and peptidoglycans were carried out by the Identification Service of the Leibniz-Institut DSMZ (Deutsche Sammlung von Mikroorganismen und Zellkulturen), Braunschweig, Germany.

Table 4. Comparison of MALDI-TOF MS identity scores using the standard clinical database and an amended database with reference profiles from S. argenteus sp. nov. and S. schweitzeri sp. nov. groups

|                    | Standard database | Amended database |
|--------------------|-------------------|-------------------|
|                    | Best hit | Identity score | Best hit | Identity score |
| S. aureus (n=22)   | S. aureus | 2.295 (0.067) | S. aureus | 2.295 (0.067) |
| S. argenteus sp. nov. (n=12) | S. aureus | 2.071 (0.102) | S. argenteus sp. nov. | 2.700 (0.066) |
| S. schweitzeri sp. nov. (n=12) | S. aureus | 1.847 (0.095) | S. schweitzeri sp. nov. | 2.676 (0.072) |

Identity score values are graded as highly probable species identification (score value 2.300–3.000), secure genus and probable species identification (2.000–2.299) and probable genus identification (1.700–1.999). Values are mean (standard deviation) of identity scores.
Table 5. Cellular fatty acid contents of *Staphylococcus aureus*, *Staphylococcus argenteus* sp. nov. and *Staphylococcus schweitzeri* sp. nov.

| Fatty acid         | 1     | 2     | 3     |
|--------------------|-------|-------|-------|
| C14:0              | 0.3   | 0.2   | 0.2   |
| C16:0              | 2.1   | 2.1   | 1.9   |
| C17:0              | 0.4   | 0.4   | 0.3   |
| C18:0              | 6.3   | 5.8   | 6.0   |
| C18:1O9c           | 2.0   | 2.4   | 2.1   |
| C18:1O7c           | 0.2   | 0.0   | 0.2   |
| C18:2O6,9c/anteiso-C18:0* | 0.8 | 0.9  | 0.7   |
| C19:0              | 0.5   | 0.4   | 0.3   |
| C20:0              | 2.6   | 1.6   | 1.7   |
| C20:1O9c           | 0.4   | 0.9   | 0.6   |
| iso-C13:0          | 0.2   | 0.0   | 0.3   |
| iso-C14:0          | 0.4   | 0.5   | 0.6   |
| iso-C15:0          | 5.4   | 7.2   | 5.8   |
| iso-C16:0          | 0.8   | 1.1   | 1.3   |
| iso-C17:0          | 3.1   | 4.6   | 4.0   |
| iso-C18:0          | 0.3   | 0.4   | 0.5   |
| iso-C19:0          | 0.9   | 1.0   | 1.0   |
| anteiso-C13:0      | 0.1   | 0.0   | 0.1   |
| anteiso-C15:0      | 50.2  | 48.5  | 47.1  |
| anteiso-C17:0      | 20.4  | 19.6  | 22.3  |
| anteiso-C19:0      | 2.9   | 2.4   | 3.2   |
| Total              | 100   | 100   | 100   |

*Differentiation between these two fatty acids was not possible.

recovered from human hosts to date (Schaumburg et al., 2012); 7) distinct clinical disease profile for *S. argenteus* sp. nov. compared to *S. aureus* (Tong et al., 2013).

Description of *Staphylococcus argenteus* sp. nov.

*Staphylococcus argenteus* (ar.gen’t.e.us. L. masc. adj. argenteus silver, silvery).

Colonies are large, 2 mm in diameter, round, convex, smooth, creamy white and demonstrate β-haemolysis on blood agar. Cells are Gram-stain-positive, coccoid, 1 μm in diameter, and form clusters. Facultatively anaerobic. Cells are catalase-positive and coagulate-positive by tube coagulate test. Biochemically positive for alkaline phosphatase, arginine dihydrolase, L-pyroroliddionyl arylamidase, galactose, maltose, mannitol, mannose, methyl β-d-glucopyranoside, sucrose, trehalose, ribose and N-acetylglucosamine, but negative for phosphatidylinositol phospholipase C, α-mannosidase, β-galactosidase, urease, alanine-phenylalanine-proline arylamidase, L-aspartic acid arylamidase, α-mannosidase, β-glucuronidase, L-leucine arylamidase, proline arylamidase, α-galactosidase, alanine arylamidase, tyrosine arylamidase, amygdalin, xylose, α-cyclodextrin, sorbitol, galactose, lactose, pullulan, raffinose and salicin (Vitek2 GP Card; bioMérieux). The peptidoglycan is of the type A3α, A11.8, L-Lys–L-Ala–(Gly)₄–5. The menaquinones MK-7, MK-8 and MK-9 are at ratios of 11·70·11 and the predominant fatty acids are anteiso-C₁₅·₀ and anteiso-C₁₇·₀.

The type strain DSM 28299T (= SSI 89.005T) was isolated from the blood culture of a 55-year-old Indigenous Australian female in 2006 in Darwin, Northern Territory, Australia. The type strain has also been deposited in the Robert Koch Institute (Germany) and the National Collection of type Cultures, Public Health England (UK).

Description of *Staphylococcus schweitzeri* sp. nov.

*Staphylococcus schweitzeri* (schwei’tzer.i. N.L. gen. n. schweitzeri of Schweitzer, named after Albert Schweitzer, founder of a hospital in Lambaréné, Gabon, and Nobel Peace Prize Laureate in 1952).

Colonies are round, 1.7 mm in diameter, convex, smooth, yellow and demonstrate β-haemolysis on blood agar. Cells are Gram-stain-positive, coccoid, 1 μm in diameter, and form clusters. Facultatively anaerobic. Cells are catalase-positive and coagulate-positive by tube coagulate test. Biochemically positive for alkaline phosphatase, arginine dihydrolase, L-pyroroliddionyl acid arylamidase, maltose, mannitol, mannose, methyl β-d-glucopyranoside, sucrose, trehalose, ribose and N-acetylglucosamine, but negative for phosphatidylinositol phospholipase C, β-galactosidase, urease, alanine-phenylalanine-proline arylamidase, L-aspartic acid arylamidase, α-mannosidase, β-glucuronidase, L-leucine arylamidase, proline arylamidase, α-galactosidase, alanine arylamidase, tyrosine arylamidase, amygdalin, xylose, α-cyclodextrin, sorbitol, galactose, lactose, pullulan, raffinose and salicin (Vitek2 GP Card; bioMérieux). The peptidoglycan is of the type A3α, A11.8, L-Lys–L-Ala–(Gly)₄–5. The menaquinones MK-7, MK-8 and MK-9 are at ratios of 7·80·13 and the predominant fatty acids are anteiso-C₁₅·₀ and anteiso-C₁₇·₀.

The type strain DSM 28299T (= SSI 89.005T) was isolated from the nares of a non-human primate (*Cercopithecus ascanius*) from Gabon, Africa within 12 h after the death of the animal in 2010. The type strain has also been deposited in the Robert Koch Institute (Germany) and the National Collection of type Cultures, Public Health England (UK).

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