

ST2249-MRSA-III: a second major recombinant methicillin-resistant *Staphylococcus aureus* clone causing healthcare infection in the 1970s

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Abstract:	<p>Typing of healthcare-associated MRSA from Australia in the 1970s revealed a novel clone, ST2249-MRSA-III (CC45), present from 1973 to 1979. This clone was present prior to the Australian epidemic caused by the recombinant clone, ST239-MRSA-III. This study aimed to characterise the genome of ST2249-MRSA-III in order to establish its relationship to other MRSA clones. DNA microarray analysis was conducted and a draft genome sequence of ST2249 was obtained. The recombinant structure of the ST2249 genome was revealed by comparisons to publicly available ST239 and ST45 genomes. Microarray analysis of genomic DNA of 13 ST2249 isolates showed gross similarities with the ST239 chromosome in a segment around the origin of replication and with ST45 for the remainder of the chromosome. Recombination breakpoints were precisely determined by the changing pattern of nucleotide polymorphisms in the genome sequence of ST 2249 isolate SK1585 compared with ST239 and ST45. One</p>

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	<p>breakpoint was identified to the right of oriC, between sites 1014 and 1065 of the gene D484_00045. Another was identified to the left of oriC, between sites 1185 and 1248 of D484_01632. These results indicate that ST2249 inherited approximately 35.3% of its chromosome from an ST239-like parent and 64.7% from an ST45-like parent. ST2249-MRSA-III resulted from a major recombination between parents that resemble ST239 and ST45. Although only limited Australian archival material is available, the oldest extant isolate of ST2249 predates the oldest Australian isolate of ST239 by three years. It is therefore plausible that these two recombinant clones were introduced into Australia separately.</p>

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6 *Staphylococcus aureus* clone causing healthcare infection in the 1970s
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Abstract

Typing of healthcare-associated MRSA from Australia in the 1970s revealed a novel clone, ST2249-MRSA-III (CC45), present from 1973 to 1979. This clone was present prior to the Australian epidemic caused by the recombinant clone, ST239-MRSA-III. This study aimed to characterise the genome of ST2249-MRSA-III in order to establish its relationship to other MRSA clones. DNA microarray analysis was conducted and a draft genome sequence of ST2249 was obtained. The recombinant structure of the ST2249 genome was revealed by comparisons to publicly available ST239 and ST45 genomes. Microarray analysis of genomic DNA of 13 ST2249 isolates showed gross similarities with the ST239 chromosome in a segment around the origin of replication and with ST45 for the remainder of the chromosome. Recombination breakpoints were precisely determined by the changing pattern of nucleotide polymorphisms in the genome sequence of ST 2249 isolate SK1585 compared with ST239 and ST45. One breakpoint was identified to the right of *oriC*, between sites 1014 and 1065 of the gene D484_00045. Another was identified to the left of *oriC*, between sites 1185 and 1248 of D484_01632. These results indicate that ST2249 inherited approximately 35.3% of its chromosome from an ST239-like parent and 64.7% from an ST45-like parent. ST2249-MRSA-III resulted from a major recombination between parents that resemble ST239 and ST45. Although only limited Australian archival material is available, the oldest extant isolate of ST2249 predates the oldest Australian isolate of ST239 by three years. It is therefore plausible that these two recombinant clones were introduced into Australia separately.

Introduction

Methicillin-resistant *Staphylococcus aureus* (MRSA) first appeared in Australia in 1965 in hospitals in Sydney¹ and Melbourne². The responsible clone, ST250-MRSA-I by multilocus sequence typing (MLST) and SCC*mec* typing, caused epidemics in numerous countries in the first global wave of MRSA^{3,4}. Contemporary phage typing and phenotypic data suggest ST250-MRSA-I was replaced in Australia in the early 1970s by another clone with chromosomal determinants for penicillinase and resistance to tetracycline, kanamycin, neomycin, erythromycin and mercury^{5,6,7}. MLST and SCC*mec* typing of isolates collected in two Melbourne hospitals in the 1970s have shown that a second multiresistant clone, ST2249-MRSA-III, a previously unrecorded member of clonal complex (CC) 45, was also present in Melbourne hospitals at least from 1973 to 1979^{2,3,4,5,6,7}.

When MLST loci are ordered by chromosomal position, ST2249 and ST45 have identical alleles at five contiguous loci (*aroE*-14, *glpF*-8, *gmk*-6, *pta*-10 and *tpiA*-3), while ST2249 and ST239 have identical alleles at two contiguous loci (*arcC*-2 and *yqiL*-3) that span the origin of replication (*oriC*)⁴. In addition, ST2249 carries a type III SCC*mec* element, located downstream of *oriC* and between *arcC* and *yqiL*, of the same type as that carried by ST239. This arrangement suggests the possibility that ST2249 arose as the result of a major chromosomal recombination involving parents that resemble ST45 and ST239. Of note, ST239 is itself the result of a major chromosomal recombination involving ST8- and ST30-like parents⁸. Such recombinations between parents of distinct genetic backgrounds that result in new multilocus sequence types are unusual in *S. aureus* with only three reported to date^{8,9}. The aim of this study is to test the hypothesis that ST2249-MRSA-III is a hybrid

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resulting from chromosomal recombination involving ST45- and ST239-like parent strains.

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Methods

Isolates

Thirteen isolates belonging to ST2249-MRSA-III were available from culture collections from two inner Melbourne teaching hospitals from the 1970s (Table 1). Nine isolates from a childrens' teaching hospital had been studied previously^{2,4,5}. Four additional isolates were obtained from a collection from an adult teaching hospital.

DNA microarray analysis

Arrays and reagents were obtained from Alere Technologies, Jena, Germany. The principle of the assay, related procedures, and a list of targets has been described previously¹⁰. Target genes included species markers, markers for accessory gene regulator (*agr*) alleles and capsule types, virulence factors, resistance genes, staphylococcal superantigen-like/exotoxin-like genes (*set/ssl* genes) and genes encoding adhesion proteins and immune evasion factors. Positive, negative and ambiguous results for individual markers including those requiring discrimination of allelic variants were interpreted as described previously¹¹. Our initial strategy was to examine microarray results for available ST2249 isolates for evidence of likely recombination and for diversity within the lineage.

dru PCR and coagulase typing

Sequencing of SCC*mec* direct repeat units (*dru*) of 10 isolates of ST2249 from 1973 to 1979⁴ was performed using the forward (GTTAGCATATTACCTCTCCTTGC) and reverse (GCCGATTGTGCTTGATGAG) primers described by Goering *et al*¹² and the gel-based method described by Tohda *et al*¹³. Coagulase restriction fragment length polymorphism (RFLP) was determined as previously described¹⁴.

Genome sequencing and data analysis

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3 Purified genomic DNA from ST2249 isolate SK1585, isolated in 1973 in Melbourne,
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5 was sheared to ~3kb using a Covaris S220 focused ultrasonicator (Covaris,
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7 Massachusetts, USA). A Mate Pair library suitable for sequencing on the IonTorrent
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9 PGM was prepared according to manufacturer's instructions, and a single 318 chip of
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11 data was generated using an Ion Torrent PGM (Life Technologies, California, USA)
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13 according to manufacturer's instructions.
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18 Reads were split into pairs with SFFextract 2.0.13, and file headers were modified
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20 with in-house perl scripts prior to *de novo* assembly with Newbler v2.6 (Roche,
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22 Connecticut, USA). Contigs were annotated with Prokka v1.4 (Prokka: Prokaryotic
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24 Genome Annotation System - <http://vicbioinformatics.com/>), and scaffolds were
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26 ordered against *S. aureus* JKD6008¹⁵ using Mauve Contig Mover Tool¹⁶. The
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28 resulting set of ordered, annotated scaffolds was deposited in Genbank
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30 (AYLT00000000), and all raw data organised under NCBI bio-project
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41 **Identification of major recombination breakpoints**

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43 The recombinant structure of the ST2249 chromosome was characterized with two
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45 separate analyses. The publicly available genome sequences of *S. aureus* strains
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47 JKD6008 and BK21252 were used as examples of ST2249's putative parents, ST239
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49 and ST45, respectively (accession numbers NC_017341 and NZ_AHJV00000000.1,
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51 respectively). Based on MAUVE analysis, these two strains were closer in overall
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53 genome content to ST2249 than other strains of similar sequence types with publicly
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55 available genome sequences.
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5 The first analysis was based on the method of Brochet *et al*¹⁷. Briefly, the contigs of
6 the draft genome sequence of ST2249 were ordered using the genome coordinates of
7 strain JKD6008. The ST2249 genome sequence was then subdivided into 500 bp,
8 non-overlapping windows and subsequently BLASTed against local databases of
9 ST239 and ST45 genome sequences. Only windows that produced a BLAST hit with
10 100% coverage and no gaps were considered. E-values of 10^{-2} , 10^{-4} , and 10^{-6} were
11 considered but these identified the same breakpoints, so 10^{-4} was selected for further
12 analysis. Windows with multiple hits to a parent and windows absent from either of
13 the two parents were discarded in order to filter out paralogs and accessory regions,
14 respectively. The number of nucleotide polymorphisms within eligible windows,
15 between ST2249 and each of its two parents, was plotted according to the ST2249
16 genome coordinates.
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34 For the second analysis, the ST2249 genome sequence was aligned with those of its
35 two putative parents using the progressiveMauve algorithm of Mauve v2.3.1¹⁸, with
36 default parameters. Locally collinear blocks (LCBs) were included in the subsequent
37 analysis provided that they contained sequence from all three strains. LCBs were
38 ordered based on the genome coordinates of strain JKD6008 and then concatenated.
39 All gapped positions were removed. A sliding window analysis was performed using
40 DnaSP v5¹⁹ to determine the number of nucleotide polymorphisms between ST2249
41 and each of its two parents, using 500 bp, non-overlapping windows, and plotting
42 these polymorphisms according to the ST2249 genome coordinates.
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3 Once the approximate breakpoint coordinates were determined, precise coordinates
4 were identified through visual inspection of the sequences. The gene sequences that
5 were identified through visual inspection of the sequences. The gene sequences that
6 contained the two major recombination breakpoints were then aligned using the
7 ClustalW algorithm, implemented in MegAlign v7.1 (Lasergene).
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Results and Discussion

Microarray analysis of genomic DNA of 13 ST2249 isolates showed general similarities with CC45/*agr* IV for most genomic markers (Table 2, supplementary Table 1 and Figure 1). "CC45/*agr* IV" refers to a lineage within CC45 that differs from the better known, more common and more widespread "CC45/*agr* I" lineage to which, among others, MRSA strains Berlin Epidemic Strain, USA 600, WA-MRSA 4 and WA-MRSA 106 belong. Differences between the two CC45 lineages include not only the *agr* group affiliation but also alleles of *fnbA/B*, *sdrD*, *vwb* and *lmrP* as well as presence of *sasG*. CC45/*agr* IV MRSA became common in Australia (WA-MRSA-23 and -84) and Hong Kong¹¹ but there are no data on the distribution of CC45/*agr* IV in the 1970s when ST2249 emerged nor on CC45/*agr* IV-MSSA in general.

However, several genes in ST2249 yielded microarray signals that were not in accordance with CC45/*agr* IV alleles but rather with CC8 alleles (*sasG* and *fnbA/B*, *sdrC/D*, *ssl/set*-locus) while others matched hybridisation patterns from CC30 (*clfB*, *lmrP*, capsule locus) (Table 2). The MLST gene *arcC* had a CC30 and ST239 sequence, while *yqiL* was identical to the sequence from CC8 and ST239. The *spa* type was identical to that of ST239 (t037). In addition, coagulase RFLP PCR revealed the same type as AUS-2 and -3 strains, both Australian variants of ST239-MRSA-III²⁰. Isolates of ST2249 collected over seven years belonged to two closely related *dru* types, 11j (six isolates from 1973 to 1977) or 9aj (seven isolates from 1976 to 1979) (Table 1). By array hybridisation, the SCC*mec* element was identified as type III, and the presence of *ccrC* and the mercury resistance operon resembled AUS-3.

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3 Assuming a constant order of genes within any *S. aureus* chromosome, these
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5 observations were in accordance with a larger fragment of CC8 origin having been
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7 inserted into a CC45/*agr* IV chromosome and a smaller fragment of CC30 origin
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9 around *oriC* having been inserted into that larger CC8 fragment. Because of the gene
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11 content similarities identified through microarray analysis, as well as similarities
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13 identified by MLST, *spa*, coagulase, *dru* and SCC*mec* typing, it was assumed that the
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15 entire insert into the CC45/*agr* IV chromosome originated from an ST239-MRSA-III
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17 strain that itself originated from a previously characterized recombination involving
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19 CC8 and CC30.
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25 In order to test this hypothesis and to more precisely characterize the genome of
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27 ST2249, one isolate, SK1585, was sequenced. Ion Torrent PGM sequencing generated
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29 1699425 read pairs (average length - 90 bp). De novo assembly with Newbler resulted
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31 in ~150 contigs that were further organised into 15 scaffolds with an N50 = 456,855
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33 bp, and a Nmax = 1,154,088 bp.
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39 Recombination breakpoints were visually detected by examining the changing pattern
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41 of nucleotide polymorphism in the ST2249 genome sequence, in comparison with the
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43 ST239 and ST45 genomes (Figure 2). Across the origin of replication, the ST2249
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45 chromosome is much more similar to the ST239 chromosome (ST2249 vs ST239:
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47 0.0000872 nucleotide polymorphisms/site) than to the ST45 chromosome (ST2249 vs
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49 ST45: 0.0175 nucleotide polymorphisms/site). However, across the remainder of the
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51 chromosome, ST2249 is much more similar to the ST45 chromosome (ST2249 vs
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53 ST45: 0.00012 nucleotide polymorphisms/site) than to the ST239 chromosome
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55 (ST2249 vs ST239: 0.014865 nucleotide polymorphisms/site) (Figure 2). The above
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3 analysis was based on BLASTN comparisons of genome sequences. Essentially the
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5 same overall pattern of similarity between ST2249 and the parent-like genomes of
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7 ST239 and ST45 was found using a Mauve alignment of genome sequences
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10 (Supplementary Figure 1).

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14 The genomic comparisons identified recombination breakpoints to the right and left of
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16 the origin of replication, which were investigated in more detail. The right
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18 recombination breakpoint occurs between sites 1014 and 1065 of the ST2249 gene
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20 D484_00045 (Figure 3). BLASTP searches indicate that this gene encodes a putative
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22 poly(glycerol-phosphate) alpha-glucosyltransferase. The left recombination
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24 breakpoint occurs between sites 1185 and 1248 of the ST2249 gene D484_01632
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26 (Figure 3). BLASTP searches indicate that this gene encodes *nasD*, which is a nitrate
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28 reductase. Both recombination breakpoints occurred within the coding sequences of
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30 the indicated genes, and the recombinations did not introduce frameshift mutations
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32 into these genes. Neither of these genes are the breakpoints of the previously
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34 identified ST239, ST34 and ST42 hybrids of *S. aureus*^{8,9}.

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41 These two recombination breakpoints indicate that ST2249 inherited approximately
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43 981.5 kb (35.3%) of its chromosome from an ST239-like parent, i.e. a CC8/CC30
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45 hybrid strain itself, and approximately 1,798 kb (65.7%) from a CC45/*agr* IV-like
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47 parent. These sizes are estimated from the draft genome sequence of the ST2249
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49 strain, SK1585. Minor uncertainties in the exact size of the parental contributions
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51 arise from potential sequencing/assembly errors, the undefined location of one
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53 scaffold that comprises ribosomal DNA operon that can be found at multiple locations
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55 across *S. aureus* genomes, and the possibility that ST2249 subsequently acquired or
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3 lost genes (described below). We have shown that ST2249-MRSA-III most probably
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5 resulted from a major recombination between parents that resemble ST239-MRSA-III
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7 and CC45/*agr* IV, although a recombination involving ST239-MSSA and CC45/*agr*
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9 IV followed by an independent acquisition of an *SCCmec* III/*mer* element might have
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11 been possible. However, this possibility seems unlikely as ST239-MSSA are very rare
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13 and ST2249-MSSA never has been described.
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18 ST2249 isolates have some unique gene content variations. The gene *bbp* (bone
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20 binding protein) that is normally located near the right recombination breakpoint was
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22 absent from the draft genome sequence of strain SK1585 and it was not detected by
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24 array hybridization in that strain. However, *bbp* was present in 12 of 13 ST2249
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26 isolates, suggesting that it has been lost in some isolates and is not related to the major
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28 recombination event. Mauve misaligned a phiSa3-like phage with phiNM3 and
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30 phiSa2 -like phage, which is visible as a spike of ST45 SNPs in the middle of the
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32 genome in Supplementary Figure 1.
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39 Although only limited Australian archival material is available, the oldest extant
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41 isolate of ST2249 predates the oldest Australian isolate of ST239 by three years⁴.
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43 Even older isolates of ST239 are known from Europe²¹. It is therefore plausible that
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45 these two recombinant clones were introduced into Australia separately, or that
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47 ST2249 emerged in Australia before the importation and spread of ST239 there was
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49 noted. While comprehensive data are lacking, the parent CC45/*agr* IV lineage appears
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51 to be more common in Asia than in either Europe or North America where it is
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53 virtually unknown (with CC45/*agr* I being dominant), thus suggesting a possible
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55 origin for ST2249.
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5 Another unanswered question is the mechanism by which such large portions of the
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7 chromosome are transferred. It is remarkable that transfer involves both core and
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9 accessory regions of the chromosome as a block of contiguous DNA, and that the
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11 recombination breakpoints can fall within genes without introducing frameshifts:
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13 these characteristics are consistent with homologous recombination. A high-frequency
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15 of recombination (Hfr-like) conjugative process remains the most likely mechanism
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17 of transfer, because of the large sizes of the transferred DNA. Recent work on patterns
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19 of recombination in the *S. aureus* chromosome has presented evidence of elevated
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21 recombination rates around the origin of replication and an association of localized
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23 recombination hotspots with integration sites of certain mobile genetic elements²².
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26 Whether or not megabase-scale and kilobase-scale recombination events are mediated
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28 through the same mechanisms of transfer is unknown. Furthermore, it is possible that
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30 more hybrid strains of *S. aureus* remain to be discovered. To date, hybrid strains have
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32 been identified based on alleles from MLST, *spa* and other strain typing schemes that
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34 are at odds with the rest of the strain's typing profile. Contemporary assays such as
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36 array hybridisation and full genome sequencing might identify more hybrid strains, by
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38 interrogating at higher resolution across the entire genome.
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45 Thus the frequency and causation of such events remains at issue. As mentioned
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47 above, only three strains have been proven to originate from genomic replacements,
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49 giving the impression that megabase-scale recombinations are very rare events in the
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51 evolution of *S. aureus*. It is therefore all the more intriguing that ST2249 was derived
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53 from two major and temporally sequential chromosomal recombinations (CC8 and
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55 CC30 to ST239; and ST239 and CC45/*agrIV* to ST2249). If these events are indeed
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3 rare and result from uncommon environmental conditions, it is remarkable that they
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5 occurred twice in the formation of ST2249.
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23 **Transparency Declaration**

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25 Stefan Monecke and Ralf Ehrlich are employed by Alere Technologies GmbH.
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3 Table 1. Origin and *dru* type of ST2249 isolates
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5 Table 2. Summary of the major differences between ST2249-MRSA-III, ST239-
6 MRSA-III, CC8, CC30, CC45 (*agr*I) and CC45 (*agr*IV) by microarray analysis.
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8 Supplementary Table 1. Comparison of microarray target results of 13 isolates of
9 ST2249-MRSA with those of one ST239-MRSA-III isolate.
10

11 Figure 1. Approximate localization of array targets in ST2249-MRSA-III isolate
12 SK1585 matching with targets found in CC8, CC30 and CC45/*agr* IV (outer circle) in
13 comparison with ST239 chromosome (inner circle).
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16 Figure 2. Comparison of single nucleotide polymorphisms (SNP) per site of ST2249-
17 MRSA-III (SK1585) with putative parents ST45 and ST239 respectively.
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20 Figure 3. Right recombination breakpoint between sites 1014 and 1065 of the ST2249
21 gene D484_00045 and left recombination breakpoint between sites 1185 and 1248 of
22 the ST2249 gene D484_01632.
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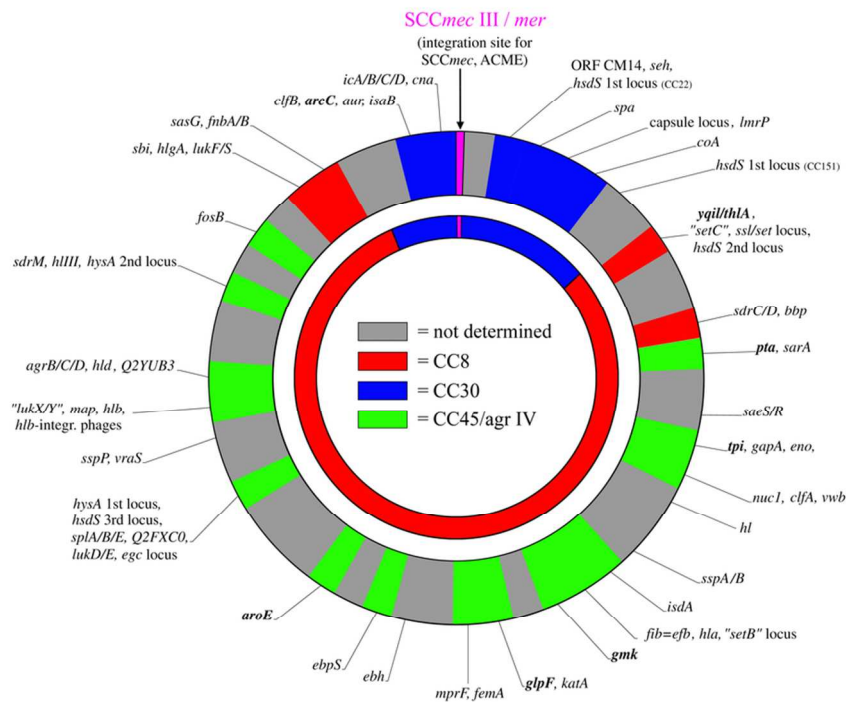
24 Supplementary Figure 1. SNP comparison of ST2249 genome with those of ST239
25 and ST45 showing Mauve misalignment of a phiSa3-like phage with phiNM3 and
26 phiSa2 -like phage as a spike in ST45 SNPs in the middle of the genome.
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Table 1. Origin and *dru* type of ST2249 isolates

Isolate	Year of isolation	City	Hospital	<i>dru</i> type
SK1585	1973	Melbourne	Childrens' teaching	dt11j
SK1814	1974	Melbourne	Childrens' teaching	dt11j
SK1821	1974	Melbourne	Childrens' teaching	dt11j
SK1696	1975	Melbourne	Childrens' teaching	dt11j
AH1413	1976	Melbourne	Adult teaching	dt9aj
AH1414	1976	Melbourne	Adult teaching	dt9aj
AH1415	1976	Melbourne	Adult teaching	dt11j
AH1431	1976	Melbourne	Adult teaching	dt9aj
SK1582	1976	Melbourne	Childrens' teaching	dt9aj
SK1717	1977	Melbourne	Childrens' teaching	dt9aj
SK1774	1977	Melbourne	Childrens' teaching	dt11j
SK1734	1978	Melbourne	Childrens' teaching	dt9aj
SK1783	1979	Melbourne	Childrens' teaching	dt9aj

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Marker	Allele/probe	ST2249-MRSA-III	ST239-MRSA-III+SCCmec	CC8	CC30	CC45 (agr I)	CC45 (agr IV)
SCCmec	III or III ^{int}	t037	III or III ^{int}	variable: 0, II, IV, V, others	variable: 0, II, IV, V, others	variable: 0, II, IV, V, others	variable: 0, IV, V,
staphylococcal protein A	8	t030, t037, t074	8	t008, t024, t190, t197	t012, t017, t018, t021	t015, t026, t050, t065	t727, t1575
capsule locus	8	8	8	8	8	8	8
staphy. exotoxin-like protein	setC	POS	POS	POS	NEG	AMB / VAR	AMB / VAR
	ssi01/set6 (COL)	POS	POS	POS	NEG	NEG	NEG
	ssi01/set6 (Mu50+N315)	AMB / VAR	AMB / VAR	AMB / VAR	NEG	NEG	NEG
	ssi01/set6 (MRSA252)	NEG	NEG	NEG	POS	AMB / VAR	AMB / VAR
	ssi01/set6 (other alleles)	NEG	NEG	NEG	NEG	AMB / VAR	AMB / VAR
staphylococcal superantigen-like protein 2	ssi02/set7	POS	POS	POS	NEG	NEG	NEG
	ssi02/set7 (MRSA252)	NEG	AMB / VAR	AMB / VAR	POS	POS	POS
staphylococcal superantigen-like protein 3	ssi03/set8 probe 1	POS	POS	POS	NEG	NEG	NEG
	ssi03/set8 probe 2	POS	POS	POS	NEG	NEG	NEG
	ssi03/set8 (MRSA252_SAR0424)	NEG	NEG	NEG	POS	NEG	NEG
staphylococcal superantigen-like protein 4	ssi04/set9	POS	POS	POS	NEG	NEG	NEG
	ssi04/set9 (MRSA252_SAR0425)	NEG	NEG	NEG	POS	POS	POS
staphylococcal superantigen-like protein 5	ssi05/set3 probe 1	POS	POS	POS	NEG	NEG	NEG
	ssi05/set3 (RF122, probe-611)	AMB / VAR	AMB / VAR	AMB / VAR	NEG	NEG	NEG
	ssi05/set3 probe 2 (612)	POS	AMB / VAR	AMB / VAR	NEG	NEG	NEG
	ssi05/set3 (MRSA252)	NEG	NEG	NEG	POS	POS	POS
staphylococcal superantigen-like protein 6	ssi06/set21	POS	POS	POS	NEG	NEG	NEG
	ssi06 (NCTC8325+MW2)	POS	POS	POS	AMB / VAR	AMB / VAR	AMB / VAR
staphylococcal superantigen-like protein 7	ssi07/set1	POS	POS	POS	NEG	NEG	NEG
	ssi07/set1 (MRSA252)	AMB / VAR	AMB / VAR	AMB / VAR	POS	NEG	NEG
	ssi07/set1 (AF188836)	NEG	AMB / VAR	NEG	AMB / VAR	AMB / VAR	POS
staphylococcal superantigen-like protein 8	ssi08/set12 probe 1	POS	POS	POS	NEG	NEG	NEG
	ssi08/set12 probe 2	POS	POS	POS	NEG	NEG	NEG
staphylococcal superantigen-like protein 9	ssi09/set5 probe 1	POS	POS	POS	NEG	NEG	NEG
	ssi09/set5 probe 2	POS	POS	POS	NEG	NEG	NEG
	ssi09/set5 (MRSA252)	NEG	NEG	NEG	POS	POS	POS
staphylococcal superantigen-like protein 10	ssi10/set4	POS	POS	POS	AMB / VAR	AMB / VAR	AMB / VAR
	ssi10 (RF122)	NEG	AMB / VAR	AMB / VAR	NEG	NEG	NEG
	ssi10/set4 (MRSA252)	AMB / VAR	AMB / VAR	AMB / VAR	POS	POS	POS
type I site-specific deoxyribonuclease subunit, 2n	hds2 (Mu50+N315+COL+USA300+N)	POS	POS	POS	NEG	NEG	NEG
	hds2 (MW2+MSSA476)	POS	NEG	AMB / VAR	NEG	NEG	NEG
	hds2 (MRSA252)	NEG	NEG	NEG	POS	POS	POS
staphylococcal superantigen-like protein 11	ssi11/set2 (COL)	POS	POS	POS	NEG	NEG	NEG
	ssi11/set2 (MRSA252)	NEG	NEG	NEG	POS	NEG	NEG
sdrC	sdrC (B1)	NEG	NEG	NEG	NEG	POS	POS
	sdrC (COL)	POS	POS	POS	NEG	NEG	NEG
	sdrC (MW2+MRSA252+RF122)	NEG	NEG	NEG	AMB / VAR	AMB / VAR	NEG
sdrD	sdrC (other than MRSA252+RF122)	POS	POS	POS	NEG	NEG	NEG
	sdrD (consensus)	POS	COMM	COMM	COMM	COMM	POS
	sdrD (COL+MW2)	POS	COMM	COMM	NEG	COMM	NEG
	sdrD (other)	NEG	NEG	NEG	NEG	NEG	POS
bbp	bbp (consensus)	COMM	COMM	COMM	COMM	COMM	COMM
	bbp (COL+MW2)	COMM	COMM	COMM	NEG	NEG	NEG
	bbp (MRSA252)	NEG	NEG	NEG	COMM	NEG	NEG
	bbp (ST45)	NEG	NEG	NEG	NEG	COMM	COMM
cfa	cfa (COL+RF122)	NEG	POS	POS	AMB / VAR	AMB / VAR	AMB / VAR
	cfa (MRSA252)	NEG	AMB / VAR	AMB / VAR	POS	NEG	NEG
	cfa (Mu50+MW2)	POS	AMB / VAR	AMB / VAR	NEG	POS	POS
vwb	vwb (consensus)	POS	COMM	POS	POS	AMB / VAR	POS
	vwb (COL+MW2)	NEG	COMM	POS	NEG	NEG	NEG
	vwb (MRSA252)	NEG	NEG	NEG	POS	POS	NEG
	isdA (MRSA252)	POS	NEG	NEG	POS	POS	POS
	isdA (other than MRSA252)	NEG	POS	POS	NEG	AMB / VAR	AMB / VAR
fibrinogen binding protein (19 kDa)	fib	NEG	POS	POS	NEG	NEG	NEG
	fib (MRSA252)	POS	NEG	NEG	POS	POS	POS
staphylococcal exotoxin-like protein, second locu	setB3	NEG	POS	POS	NEG	NEG	NEG
	setB3 (MRSA252)	POS	NEG	NEG	POS	POS	POS
	setB2	NEG	POS	POS	NEG	NEG	NEG
	setB2 (MRSA252)	NEG	NEG	NEG	POS	AMB / VAR	AMB / VAR
	setB1	AMB / VAR	POS	POS	POS	NEG	NEG
defensin resistance protein	mprF (COL+MW2)	NEG	POS	POS	AMB / VAR	NEG	NEG
	mprF (Mu50+MRSA252)	NEG	AMB / VAR	AMB / VAR	POS	AMB / VAR	AMB / VAR
cell wall associated fibronectin-binding protein	ebp5_probe 612	NEG	POS	POS	POS	NEG	NEG
	ebp5 (01-1111)	POS	NEG	NEG	NEG	POS	POS
	ebp5 (COL)	NEG	POS	POS	NEG	NEG	NEG
hyaluronate lyase, first / second locus	hysA1 (MRSA252)	NEG	NEG	NEG	NEG	NEG	NEG
type I site-specific deoxyribonuclease subunit, 3n	hds3 (all other than RF122+ MRSA252)	POS	POS	POS	NEG	NEG	POS
	hds3 (COL+USA300+NCTC8325+MW2)	POS	POS	POS	NEG	NEG	NEG
	hds3 (CC51+ MRSA252)	POS	NEG	NEG	POS	NEG	POS
	hds3 (MRSA252)	NEG	NEG	NEG	POS	NEG	NEG
serin- protease E	splE	NEG	COMM	POS	POS	NEG	NEG
serin- protease B	splB	NEG	COMM	POS	NEG	NEG	NEG
serin- protease A	splA	NEG	COMM	POS	NEG	NEG	NEG
hypothetical protein, located next to serine protease	Q2FXC0	NEG	POS	POS	NEG	NEG	NEG
leukocidin D / E	lukD/E	NEG	COMM	POS	NEG	NEG	NEG
egc cluster	map (COL)	POS	NEG	NEG	NEG	POS	POS
	map (MRSA252)	POS	POS	POS	NEG	NEG	NEG
	map (Mu50+MW2)	NEG	AMB / VAR	AMB / VAR	COMM	POS	POS
leukocidin/ haemolysin toxin family protein	lukX (lukB)	NEG	POS	POS	AMB / VAR	POS	POS
leukocidin/haemolysin toxin family protein	lukY (lukA)	NEG	POS	POS	NEG	NEG	NEG
	lukY (ST30+ST45)	POS	NEG	NEG	POS	POS	POS
Unspecific efflux/trans-porter	Q2YUB3	AMB / VAR	AMB / VAR	AMB / VAR	NEG	NEG	NEG
accessory gene regulator	agrI	NEG	POS	POS	NEG	POS	AMB / VAR
	agrIII (total)	NEG	NEG	NEG	POS	NEG	NEG
	agrIV (total)	POS	AMB / VAR	NEG	NEG	NEG	POS
	hIII (other than RF122)	NEG	POS	POS	POS	NEG	NEG
hyaluronate lyase, second locus	hysA2 (all other than MRSA252)	NEG	POS	POS	NEG	AMB / VAR	AMB / VAR
	hysA2 (COL+USA300+NCTC8325)	POS	POS	POS	POS	NEG	POS
	hysA2 (all other than COL+USA300+N)	NEG	NEG	NEG	POS	POS	NEG
	hysA2 (all other than COL+USA300+N)	AMB / VAR	NEG	NEG	POS	NEG	AMB / VAR
	hysA2 (MRSA252)	NEG	NEG	NEG	POS	NEG	NEG
metallothiol transferase	fosB	NEG	POS	POS	POS	NEG	NEG
haemolysin gamma / leukocidin, component C	lukS	POS	POS	POS	POS	AMB / VAR	AMB / VAR
	lukS (ST22+ST45)	AMB / VAR	AMB / VAR	AMB / VAR	AMB / VAR	POS	POS
	sasG (COL+Mu50)	POS	POS	POS	NEG	NEG	NEG
	sasG (MW2)	NEG	NEG	NEG	NEG	NEG	POS
	sasG (other than MRSA252+RF122)	POS	POS	POS	NEG	NEG	POS
	fnbB (COL)	POS	COMM	COMM	NEG	NEG	NEG
	fnbB (COL+Mu50+MW2)	AMB / VAR	RARE	AMB / VAR	RARE	VAR	AMB / VAR
	fnbB (Mu50)	NEG	AMB / VAR	AMB / VAR	RARE	VAR	NEG
	fnbB (MW2)	AMB / VAR	NEG	NEG	NEG	NEG	NEG
	fnbB (ST15)	NEG	NEG	NEG	NEG	AMB / VAR	NEG
	fnbB (ST45-2)	NEG	NEG	NEG	NEG	NEG	POS
	fnbA (COL)	POS	COMM	POS	NEG	NEG	NEG
	fnbA (MRSA252)	NEG	NEG	NEG	POS	NEG	POS
	fnbA (Mu50+MW2)	NEG	NEG	NEG	POS	POS	NEG
	cIFB (COL+Mu50)	NEG	NEG	NEG	NEG	NEG	NEG
	cIFB (MW2)	NEG	NEG	NEG	NEG	POS	POS
	cIFB (RF122)	AMB / VAR	POS	NEG	AMB / VAR	AMB / VAR	AMB / VAR
aureolysin	aur (consensus)	POS	POS	POS	POS	AMB / VAR	POS
	aur (other than MRSA252)	NEG	NEG	POS	NEG	NEG	NEG
	aur (MRSA252)	POS	POS	NEG	NEG	NEG	POS
immunodominant antigen B	isaB	NEG	NEG	POS	NEG	NEG	NEG
	isaB (MRSA252)	POS	POS	AMB / VAR	POS	POS	POS
collagen-binding adhesin	cna	POS	POS	NEG	POS	POS	POS

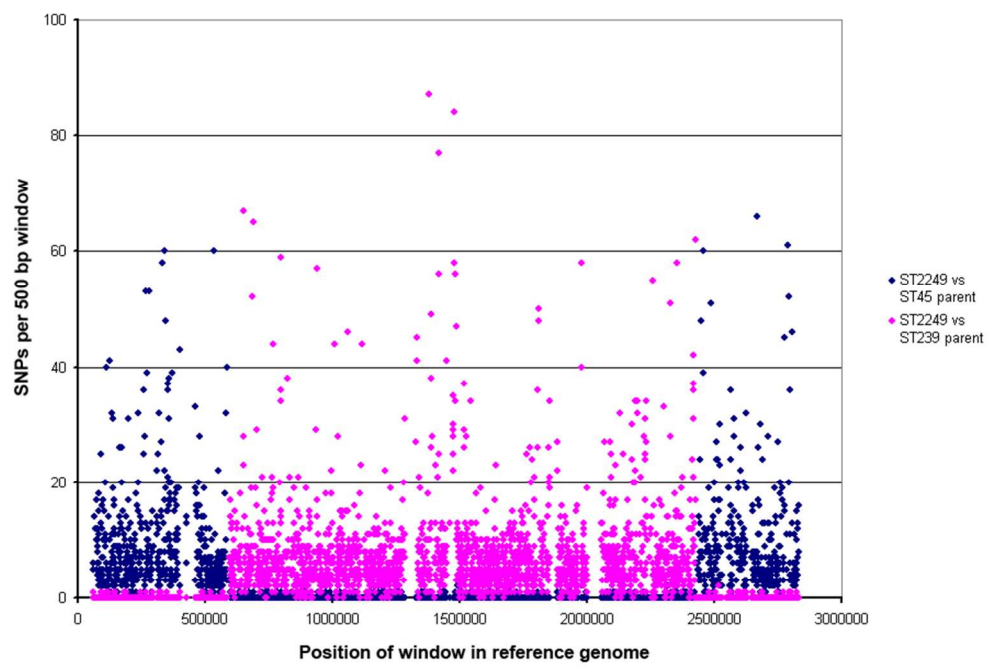


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Review

ISOLATE

>ST2249-MRSA-III

AUSTR_AH1413

AUSTR_AH1414

AUSTR_AH1415

AUSTR_AH1431

AUSTR_AH1438

AUSTR_SK1582

AUSTR_SK1585_ST2249-III

AUSTR_SK1696

AUSTR_SK1717

AUSTR_SK1734

AUSTR_SK1774

AUSTR_SK1783

AUSTR_SK1814

AUSTR_SK1821

>ST239-MRSA-III+SCCmer+ccrC, Vienna/Hungarian/Brazilian Clone

ATCC BAA-39, GenBank AEEK, Hybridisation pattern predicted from genome sequence

CUHK_HK2007, GenBank JFFV, Hybridisation pattern predicted from genome sequence

MRGR3, GenBank AHZL, Hybridisation pattern predicted from genome sequence

PPUKM-332-2009, GenBank AMRC, Hybridisation pattern predicted from genome sequence

TW20, GenBank FN433596, Hybridisation pattern predicted from genome sequence

Z172, GenBank CP006838, Hybridisation pattern predicted from genome sequence

AUSTR_SK1745

UK-EMRSA-1

UK-EMRSA-4

UK-EMRSA-7

UK-EMRSA-9

>CC45/agrIV-MSSA

Strain 21252, GenBank AHJV, Hybridisation pattern predicted from genome sequence

09V1583 (isolate from Dresden, Germany)

>CC45/agrIV-MRSA-IV, WA MRSA-23

AUSTR_04-16679 (WA23 type strain)

>CC45/agrIV-MRSA-VT, WA MRSA-84

AUSTR_07-16502 (WA84 type strain)

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spa	SPECIES MARKER			
	Domain 1 of 23S-rRNA	glyceraldehyde 3-phosphate dehydrogenase	katalase A	coagulase
	Ribos. STAU	gapA	katA	CoA
	POS	POS	POS	POS
	POS	POS	POS	POS
	POS	POS	POS	POS
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t037	POS	POS	POS	POS
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t1081	POS	POS	POS	POS
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t1575	POS	POS	POS	POS
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t1081	POS	POS	POS	POS

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accessory gene regulator allele III		accessory gene regulator allele IV		haemolysin delta	alternate penicillin binding protein 2,	truncated signal transducer protein	glycerophosphoryl diester phosphodi-	cassette chromosome recombinase genes A/B-1	
agrIII (total)	agrIV (total)	hld	mecA	delta_mecR	ugpQ	ccrA-1	ccrB-1		
NEG	POS	POS	POS	POS	POS	POS	NEG	AMB	
NEG	POS	POS	POS	POS	POS	POS	NEG	AMB	
NEG	POS	POS	POS	POS	POS	POS	NEG	NEG	
NEG	POS	POS	POS	POS	POS	POS	NEG	NEG	
NEG	POS	POS	POS	POS	POS	POS	NEG	NEG	
NEG	POS	POS	POS	POS	POS	POS	NEG	POS	
NEG	AMB	POS	POS	POS	POS	POS	NEG	NEG	
NEG	POS	POS	POS	POS	POS	POS	NEG	POS	
NEG	POS	POS	POS	POS	POS	POS	NEG	NEG	
NEG	POS	POS	POS	POS	POS	POS	NEG	NEG	
NEG	POS	POS	POS	POS	POS	POS	NEG	NEG	
NEG	POS	POS	POS	POS	POS	POS	NEG	AMB	
NEG	POS	POS	POS	POS	POS	POS	NEG	AMB	
NEG	POS	POS	POS	POS	POS	POS	NEG	NEG	
NEG	NEG	POS	POS	POS	POS	POS	NEG	NEG	
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NEG	NEG	POS	POS	POS	POS	POS	NEG	NEG	
NEG	NEG	POS	POS	POS	POS	POS	NEG	NEG	
NEG	NEG	POS	POS	POS	POS	POS	NEG	NEG	
NEG	AMB	POS	POS	NEG	POS	POS	NEG	POS	
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NEG	NEG	POS	POS	POS	POS	POS	NEG	POS	
NEG	NEG	POS	POS	POS	POS	POS	NEG	AMB	
NEG	AMB	POS	POS	POS	POS	POS	NEG	POS	
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For Peer Review

							RESISTA
cassette chromosome recombinase genes "ccrAA" (hypothetical) and ccrC			cassette chromosome recombinase genes A/B-4		SCCmec XI		beta-lactamase
MRSAZH47)	MRSAZH47)	ccrC (85-2082	ccrA-4	ccrB-4	mecC	blaZ-SCCmec XI	blaZ
NEG	AMB	POS	NEG	NEG	0	0	POS
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LS-ANTIBIOTICS						RESISTANCE : AMINOGLYS	
probable lysylphosphatidylglycerol	virginiamycin A acetyltransferase	acetyltransferase inactivating streptogramin	ATP binding protein, streptogramin-A-resistance		virginiamycin B hydrolase	bifunctional enzyme Aac/Aph, gentamicin	aminoglycoside adenylyltransferase,
mpbBM	vatA	vatB	vga	vgaA	vgb	aacA-aphD	aadD
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OSIDES	RESISTANCE						
	3'5'-aminoglycoside phosphotransferase,	streptothricine-acetyltransferase	dihydrofolate reductase type 1	fusidic acid resistance	hypothetical protein associated with fusidic	mupirocin resistance protein	tetrazyklin-resistance
aphA3	sat	dfrA	far1	Q6GD50 (fusC)	mupR	tetK	tetM
POS	POS	NEG	NEG	NEG	NEG	POS	POS
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	RESISTANCE : EFFLUX SYSTEMS						
transferase	quaternary ammonium compound resistance	quaternary ammonium compound resistance protein C					
fosB-plasmid	qacA	qacC	qacC (cons)	qacC (equine)	qacC (SA5)	qacC (Ssap)	qacC (ST94)
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	RESISTANCE : GLYCOPEPTIDES			VIRULENCE : TOX.SCHOCK.TOXIN			
Transport- /Effluxprotei n	vancomycin resistance gene	vancomycin resistance gene from enterococci	teicoplanin resistance gene from enterococci	toxic shock syndrome toxin 1			enterotoxin A
tetEfflux	vanA	vanB	vanZ	t1 (consensu	("human" all	("bovine" all	entA
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VIRULENCE : ENTEROTOXINS

enterotoxin I	enterotoxin J	enterotoxin K	enterotoxin L	enterotoxin M	enterotoxin N		enterotoxin O
entI	entJ	entK	entL	entM	entN (cons)	(other than R)	entO
POS	NEG	NEG	NEG	POS	POS	POS	POS
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egc cluster	enterotoxin Q	enterotoxin R	Enterotoxin U and/or Y	enterotoxin-like protein ORF CM14		haemolysin gamma / leukocidin, component	haemolysin leukocidin, component
egc (total)	entQ	entR	entU	entCM14 prob	entCM14 prob	lukF	lukS
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VIRULENCE : HLG AND LEUKOCIDINS							
h gamma / component C	h gamma, component	Panton Valentine leukocidin F component	Panton Valentine leukocidin S component	F component from hypothetical	S component from hypothetical	leukocidin D component	leukocidin E component
lukS (ST22+ST4)	hlgA	lukF-PV	lukS-PV	lukF-PV (P83)	lukM	lukD	lukE
POS	POS	NEG	NEG	NEG	NEG	NEG	NEG
AMB	POS	NEG	NEG	NEG	NEG	NEG	NEG
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			VIRULENCE : HAEMOLYSINS				
leukocidin/ haemolysin toxin family protein	leukocidin/haemolysin toxin family protein		putative membrane protein	haemolysin alpha	putative membrane protein		
lukX	lukY	ky (ST30+ST4)	hl	hla	hlIII (cons)	other than R	hIb-probe 1
NEG	NEG	POS	POS	POS	POS	NEG	NEG
NEG	NEG	POS	AMB	POS	POS	NEG	NEG
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			VIRULENCE : HLB-CONV PHAGES			VIRULENCE : EXFOL.T	
haemolysin beta			staphylo-kinase	chemotaxis-inhibiting protein (CHIPS)	Staphyl. Comple-ment inhibitor	exfoliative toxin serotype A	exfoliative toxin serotype B
h1b-probe 2	h1b-probe 3	n-truncated h	sak	chp	scn	etA	etB
NEG	NEG	POS	NEG	NEG	NEG	NEG	NEG
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	VIRULENCE : PROTEASES						
ACME-locus: arginine/ornithine- antiporter	aureolysin			serin- protease A	serin- protease B	serin- protease E	glutamylendopeptidase
arcD-SCC	aur (cons)	other than MRSA	aur (MRSA252)	splA	splB	splE	sspA
POS	POS	NEG	POS	NEG	NEG	NEG	POS
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AMB	POS	NEG	POS	NEG	NEG	NEG	POS
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staphopain B, protease			staphopain A (staphylopain A), protease					staphyl. exotoxin-like protein	
sspB	sspP (cons)	(other than S	setC	set6-var1_11	set6-var2_11	set6-var1_12	set6-var2_12		
POS	POS	POS	POS	POS	POS	AMB	NEG		
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staphylococcal superantigen-like protein 1

set6-var4_11	ssl01-RF122	ssl01/set6 (CO	set6 (Mu50+	set6 (MW2+M1	set6 (MRSA01	set6 (RF12	set6 (other a
POS	NEG	POS	AMB	NEG	NEG	NEG	NEG
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VIRULENCE : STA							
staphylococcal superantigen-like protein 2		staphylococcal superantigen-like protein 3			staphylococcal superantigen-like protein 4		staphylo
ssl02/set7	2/set7 (MRSA)	3/set8_prob	3/set8_prob3 (MRSA252,	ssl04/set9	3 (MRSA252,	5/set3_prob	
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STAPHYLOCOCCAL SUPERANTIGEN/ENTEROTOXIN-LIKE GENES (SET/SSL)							
staphylococcal superantigen-like protein 5			staphylococcal superantigen-like protein 6		staphylococcal superantigen-like protein 7		
set3 (RF122, pr	set3_probe 2	set3 (MRSA	ssl06/set21	(NCTC8325+)	ssl07/set1	set1 (MRSA	set1 (AF188
AMB	POS	NEG	POS	POS	POS	AMB	AMB
AMB	POS	NEG	POS	AMB	POS	AMB	AMB
NEG	POS	NEG	POS	POS	POS	AMB	NEG
AMB	POS	NEG	POS	POS	POS	AMB	NEG
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staphylococcal superantigen-like protein 8		staphylococcal superantigen-like protein 9			staphylococcal superantigen-like protein 10		
8/set12_prob	8/set12_prob	9/set5_prob	9/set5_prob	9/set5 (MRSA)	ssl10/set4	ssl10 (RF122)	10/set4 (MRSA)
POS	POS	POS	POS	NEG	POS	AMB	AMB
POS	POS	POS	POS	NEG	POS	NEG	AMB
POS	POS	POS	POS	NEG	POS	NEG	NEG
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staphylococcal superantigen-like protein 11								staphylococcal exotoxin-like protein, second															
i11/set2 (CO)				set2 (Mu50)				set2 (MW2+MS)				set2 (MRSA)				setB3		tB3 (MRSA25)		setB2		tB2 (MRSA25)	
POS	NEG	NEG	NEG	NEG	NEG	POS	NEG	AMB															
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ocus	Capsule type 1	capsular poly-saccharide synthesis	O-antigen poly-merase	capsular poly-saccharide biosyn-	Capsule type 5	capsular poly-saccharide synthesis
setB1	cap 1	capH1	capJ1	capK1	cap 5	capH5
POS	NEG	NEG	NEG	AMB	NEG	NEG
AMB	NEG	NEG	NEG	NEG	NEG	NEG
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intercellular adhesion protein C	biofilm PIA synthesis protein D	surface protein involved in biofilm	bone sialoprotein-binding protein				
icaC	icaD	bap	bbp	bbp (cons)	bp (COL+MW)	bp (MRSA252)	bbp (Mu50)
POS	POS	NEG	POS	POS	POS	NEG	NEG
POS	POS	NEG	POS	POS	POS	NEG	NEG
POS	POS	NEG	NEG	NEG	NEG	NEG	NEG
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clumping factor A							
bbp (RF122)	bbp (ST45)	clfA	clfA (cons)	FA (COL+RF122)	FA (MRSA252)	FA (Mu50+MV)	clfB
NEG	AMB	POS	POS	AMB	NEG	POS	POS
NEG	NEG	POS	POS	AMB	NEG	POS	POS
NEG	NEG	POS	POS	NEG	NEG	POS	POS
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NEG	NEG	POS	POS	AMB	NEG	POS	POS
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NEG	NEG	POS	POS	AMB	NEG	POS	POS
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clumping factor B				collagen-binding adhesin	cell wall associated fibronectin-binding	cell surface	
clfB (cons)	fb (COL+Mu5)	clfB (MW2)	clfB (RF122)	cna	ebh (cons)	ebpS	bpS_probe 61
POS	NEG	NEG	POS	POS	POS	POS	NEG
POS	NEG	NEG	POS	POS	POS	POS	NEG
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ADHAESION FACTOR							
elastin binding protein			enolase	fibrinogen binding protein (19 kDa)		fimbriae	
ebpS_probe 61	ebpS (01-1111)	ebpS (COL)	eno	fib	fib (MRSA252)	fnbA	fnbA (cons)
POS	POS	NEG	POS	NEG	POS	POS	POS
POS	POS	NEG	POS	NEG	POS	POS	POS
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POS	AMB	NEG	POS	NEG	AMB	POS	POS
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S / GENES ENCODING MICROBIAL SURFACE COMPONENTS RECOGNIZING ADHESIVE MATRIX MOLECULES							
bronectin-binding protein A				fibronectin-binding p			
fnbA (COL)	fbaA (MRSA25	fbaA (Mu50+MV	fbaA (RF122)	fnbB	fnbB (COL)	(COL+Mu50+	fnbB (Mu50)
POS	NEG	NEG	NEG	POS	POS	AMB	AMB
POS	NEG	NEG	NEG	POS	POS	AMB	NEG
POS	NEG	NEG	NEG	POS	POS	AMB	NEG
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(MSCRAMM GENES)							
Protein B			Major histocompatibility complex class II analog protein (=Extracellular adherence protein, eap)				Staphy
fnbB (MW2)	fnbB (ST15)	fnbB (ST45-2)	map	map (COL)	map (MRSA25)	p (Mu50+MV)	sasG
AMB	NEG	NEG	POS	NEG	POS	NEG	POS
AMB	NEG	NEG	POS	NEG	POS	NEG	POS
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Staphylococcus aureus surface protein G			Ser-Asp rich fibrinogen-/bone sialoprotein-binding				
sG (COL+Mu5)	sasG (MW2)	OtherThan25	sdrC	sdrC (cons)	sdrC (B1)	sdrC (COL)	sdrC (Mu50)
POS	NEG	POS	POS	POS	NEG	POS	NEG
POS	NEG	POS	POS	POS	NEG	POS	NEG
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POS	AMB	POS	POS	POS	NEG	POS	NEG
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protein C							
Ser-Asp rich fibrinogen-/bone sialoprotein-binding protein D							
V2+MRSA252	OtherThan252	sdrD	sdrD (cons)	rD (COL+MW)	sdrD (Mu50)	sdrD (other)	vwb
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					IMMUNOD.AG.B		DEFENSIN
van Willebrand factor binding protein					immunodominant antigen B		defensin r prot
vwb (cons)	vwb (COL+MW)	vwb (MRSA25)	vwb (Mu50)	vwb (RF122)	isaB	aB (MRSA25)	rF (COL+MW)
POS	NEG	NEG	NEG	NEG	NEG	POS	NEG
POS	NEG	NEG	NEG	NEG	NEG	POS	NEG
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V RESIST.	TRANSFERRIN BINDING PROT			PUTATIVE TRANSPORTER			
Resistance protein	transferrin-binding protein			hypothetical protein, similar to integral membrane protein LmrP			
prF (Mu50+25)	isdA (cons)	dA (MRSA25)	Other Than MR	Other Than R	Other Than R	lmrP (RF122)	lmrP (RF122)
POS	POS	POS	AMB	POS	POS	NEG	NEG
NEG	POS	POS	AMB	POS	POS	NEG	NEG
NEG	POS	POS	NEG	POS	POS	NEG	NEG
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AMB	POS	NEG	POS	POS	POS	NEG	NEG
AMB	POS	AMB	POS	POS	POS	NEG	NEG
AMB	POS	NEG	POS	POS	POS	NEG	NEG
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SPECIFICITY PROTEIN					MISCELLANEOUS GENES		
base subunit, 3rd locus		type I site-specific deoxyribonuclease subunit, unknown locus			hypothetical protein, located next to serine	Unspecific efflux/trans- porter	hypothetical protein
hsdS3-CC51+25	hsdS3-MRSA25	hsdSx-CC25	hsdSx-CC15	hsdSx-etd	Q2FXC0	Q2YUB3	Q7A4X2
POS	NEG	POS	AMB	POS	NEG	POS	POS
POS	NEG	POS	NEG	POS	NEG	AMB	POS
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HYALURONATE LYASE						
hyaluronate lyase, first / second locus			hyaluronate lyase, second locus			
SA1 (MRSA29+RF122) and	29+RF122) and/or	122) and/or	Other Than 12	2 (COL+USA300+N	her Than COL+US	rThan COL+U
NEG	POS	POS	AMB	POS	NEG	AMB
NEG	POS	POS	NEG	POS	NEG	AMB
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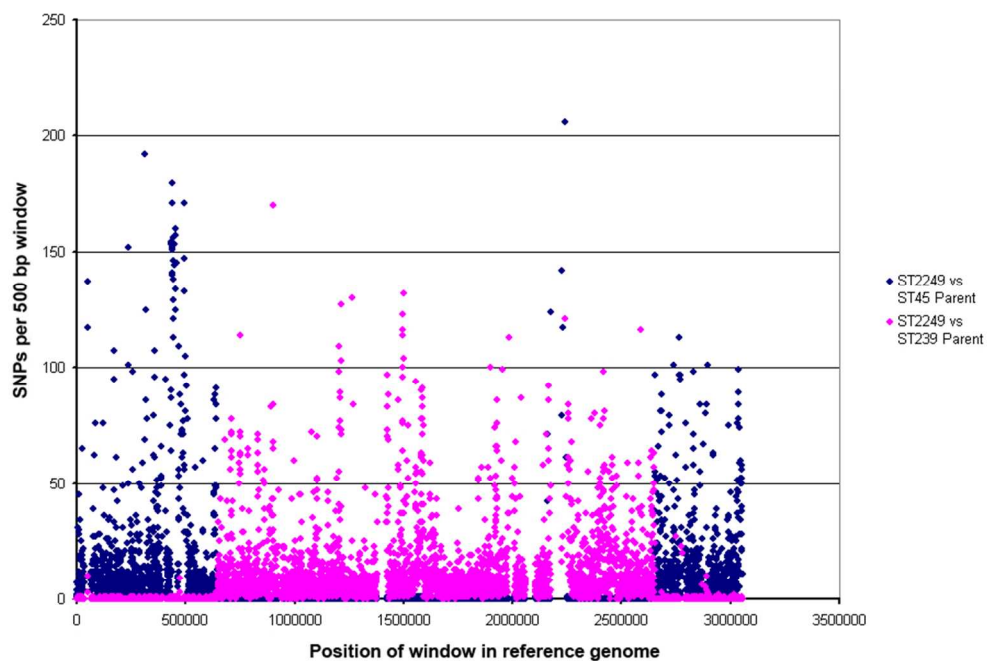
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