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Analysis of the genome sequence of the hedgehog-associated *mecC*-MRSA CC599

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Abstract

After the discovery of *mecC*, an alternative gene conferring beta-lactam resistance to *Staphylococcus (S.) aureus*, epidemiological studies suggested a zoonotic background of *mecC*-MRSA. These strains are associated with hedgehogs (*Erinaceus europaeus*) where they appear to have evolved under selective pressure exerted by penicillin-producing dermatophytes (*Trichophyton erinacei*). CC599 is one *mecC*-MRSA lineage and the aim of this study was to characterise it further.

Four genome sequences of CC599-MRSA-XI isolates from three hedgehogs from Jena, Thuringia, were obtained by nanopore sequencing. One isolate originated from a nasopharyngeal swab of a road-killed hedgehog. The second isolate was cultured from homogenised ticks collected from a gravely ill hedgehog. Because of morphological differences, two subclones were sequenced. A third isolate came from a hedgehog that was infected with *T. erinacei* as well as with CC130- and CC599-MRSA.

The studied isolates carried SCC*mec* XI elements identical to those from other *mecC*-MRSA lineages. This also included a specific penicillinase gene and an arsenic resistance operon. Isolates carried two pathogenicity islands, one of them harbouring genes for enterotoxins C and L (*sec, sel*), and for the toxic shock syndrome toxin (*tst1*). Other virulence factors included enterotoxin genes *seli2=sel26* and *selu2=sel27* as well as leukocidin genes *lukD/E*. The prophage carriage was variable. Mitomycin C induction followed by nanopore sequencing and transmission electron microscopy yielded *Dubowvirus*-like particles as well as particles with the *tst1/sec/sel* pathogenicity island.

Among 65 hedgehogs sampled in 2024-2026 in and around Jena, seven had *mecC*-MRSA. In addition, three cases of *mecC*-MRSA were identified by random sampling in the years before. Five hedgehogs carried CC599-MRSA-XI; four, CC130-MRSA-XI and one had both MRSA

strains. CC599-MRSA-XI has also been found in humans, but this is rare. No CC599 isolate was found among 1,800 clinical MRSA isolates collected over 20 years at Dresden University Hospital. Among 3,000 MRSA collected 2010 to 2019 at Regensburg University Hospital, five belonged to this strain while a second sampling period, 2020 to 2024 yielded as many as six CC599-MRSA-XI among a total of 518 MRSA isolates. Some human isolates differed from hedgehog isolates, either in an absence of the *tst1/sec/sel* pathogenicity island, or in a presence of a CRISPR/*cas* operon localised downstream of SCC*mec*.

In conclusion, CC599-MRSA-XI is a hedgehog-associated *mecC*-MRSA strain. It carries virulence factors that are also relevant to humans, and it may have zoonotic potential.

Introduction

Staphylococcus aureus is a ubiquitous bacterium that colonises 20-30% of the human population [1] as well as a wide variety of wild [2, 3] and domestic animals. Beyond mere carriage, *S. aureus* causes a wide range of infections, such as skin and soft tissue infections (SSTI) including mastitis, bone, joint and implant infections, pneumonia, septicaemia, and various toxicoses.

Shortly after penicillin was introduced, in the 1940s, the first penicillinase-producing *S. aureus* strains were detected. This led to the development of penicillinase-stable semi-synthetic compounds such as oxacillin and methicillin, and first/second generation cephalosporins. Within a year after the introduction of "Celbenin", methicillin-resistant *S. aureus* (MRSA) was reported in the United Kingdom (UK) [4]. This resistance is due to a modified penicillin-binding protein (PBP2′ or PBP2a) encoded by the *mecA* gene. The presence of PBP2a confers resistance to all beta-lactam antibiotics except for two very recently developed compounds, ceftobiprole [5] and ceftaroline. The *mecA* gene is located on complex mobile genetic elements, known as SCC*mec* (staphylococcal cassette chromosome or staphylococcal chromosomal cassette) carrying *mecA*. In addition to *mecA*, SCC*mec* elements comprise recombinase genes, regulatory elements and, variably, additional genes encoding resistance to other antimicrobials, such as aminoglycosides or macrolides, and to heavy metal ions [6-8]. In 2010, however, two Irish patients were identified with methicillin-resistant, *mecA*-negative isolates assigned to a *S. aureus* lineage known as clonal complex (CC) CC130, while the same phenomenon was also observed in CC425 strains from English and Danish cattle. This led to intensive sequencing efforts and the description of a new gene associated with beta-lactam resistance in *S. aureus*, *mecC*, situated on a novel SCC*mec* element, SCC*mec* XI. There, it is accompanied, among other genes, by its regulatory genes, by a specific beta-lactamase gene, an arsenic resistance operon, as well as by *ccr r*ecombinase genes [9, 10]. In the following years, *mecC*-MRSA was identified in various animal species (including hedgehog, cattle, sheep, dog, otter, cat, lynx, harbour seal, guinea pig, rabbit, hare, rat, shrew, chaffinch, magpie, cinereous vulture) as well as from humans [3, 11-26]. However, apart from cases of an Australian domestic cat [27] and a

Japanese race horse [28], *mecC*-MRSA appeared to be restricted to Western Europe. The majority of reports described CC130-MRSA-XI, but there were also reports of CC599-MRSA-XI from cattle from Belgium [29], from a domestic cat from Germany [30], and of a human case from the Dutch/German border region [31].

With the description of CC130-MRSA-XI as causative agent in two cases of fatal/terminal disease in Swedish hedgehogs [32], these animals gained attention as a possible natural host of *mecC*-MRSA. Subsequent studies from Sweden and Denmark showed carriage rates of *mecC*-MRSA in hedgehogs of more than 60% [24, 33].

An explanation for the phenomenon of MRSA in hedgehogs was, remarkably, provided already some 60 years earlier at the far side of the world. In the 1960ies, Smith and Marples, isolated penicillin-resistant *S. aureus* from European hedgehogs in New Zealand, where it is an invasive species introduced by European settlers in the second half of the 19th century [34]. These isolates were described as oxacillin-susceptible, and thus the resistance was attributed to the presence of penicillinase [35]. Given that *mecC*-positive strains present with low minimal inhibitory concentrations for oxacillin [10, 11, 36, 37], a presence of *mecC* cannot safely be ruled out in retrospect. Most interestingly, these animals were co-colonized with a dermatophyte, *Trichophyton erinacei*. Thus, Smith and Marples performed experiments showing a production by *T. erinacei* of a substance that inhibited the *in vitro* growth of penicillin-susceptible *S. aureus* strains and that could be neutralized by penicillinase [35, 38, 39]. Indeed, more recent work demonstrated a presence of bencylpenicillin (and 6-(5-hydroxy-*n*-valeramido)-penicillanic acid) in cultures of *T. erinacei* by ultra-high-performance liquid chromatography-tandem mass spectrometry [40] and liquid chromatography-mass spectrometry [34]. In addition, the gene cluster responsible for its synthesis was identified by whole genome sequencing [34, 40].

Genotypic characterisation of *mecC*-MRSA from hedgehogs across Europe and New Zealand assigned these strains to six different clonal complexes, CC49 [34, 41], CC130 [3, 24, 32-34, 40-43], CC425 [34, 40], CC599 [3, 34], CC1943 including ST2361 [24, 33, 34, 40, 41, 43] and CC2616

[34]. In a large European sequencing study, CC130 appeared to be the most common *mecC*-MRSA lineage (contributing 75% of isolates), followed by CC1943 (15%), CC2616 (6%), CC425 (3%), CC49 (1%, which uniquely was also found in New Zealand) and CC599 (1%) [34].

The analysis of the phylogeny of CC130, CC425 and CC1943 placed the estimated dates for the most recent common ancestor of various sub-lineages within these clonal complexes back into the first half of the 20th century (for most sub-lineages within CC130 and CC425) or, respectively, into the 19th century, possibly, even earlier (CC1943). This means, that the evolution and emergence of *mecC*-MRSA predated the use of beta-lactam compounds in human medicine. Thus, was a result of the co-evolution of hedgehogs, *S. aureus* and *T. erinacei* as well as of the selective pressure exerted by penicillin-producing dermatophytes on other microorganisms in the same ecological niche. As consequence, a *S. aureus* strain might gain only a permanent foothold in a hedgehog niche if it acquired a, horizontally transmissible, SCC*mec* XI element. Indeed, many of the hedgehog-associated *mecC*-MRSA lineages have beta-lactam susceptible precursors that infect/colonise other mammals. CC49-MSSA occurs in rodents [44, 45], CC130-MSSA is a lineage native to small ruminants, *i.e*., sheep and goats [46-48] while CC425 is associated with large ruminants, cattle and cervids [10, 49] as well as badgers [50]. CC1943-MSSA have sporadically been described from hedgehogs [34, 41], however, and for CC599 and CC2616 is, to the best of our knowledge, nothing known on MSSA precursor strains.

Following a detection of a CC599 strain in a road-killed hedgehog, we sequenced that isolate in order to further characterise this arguable least known *mecC*-MRSA lineage. In addition, we started to screen hedgehogs from a local, Thuringian, hedgehog rehabilitation centre and to look for CC599 microarray profiles and/or genome sequences in datasets from hospital settings, in Regensburg, Bavaria, and Dresden, Saxony. This allowed to assess the variability within the lineage also with regard to virulence factors that can play a role in pathogenesis in humans.

Materials and methods

Strains and isolates

Swabs were cultured in parallel on Columbia agar with 5% sheep blood (Becton Dickinson, Heidelberg, Germany) and on Baird-Paker agar (by Oxoid, via Fisher Scientific, Schwerte, Germany). Isolates were re-cloned on Columbia blood agar, and their identification as *S. aureus*/MRSA was confirmed by MALDI-TOF (MALDI Biotyper, Bruker-Daltonics, Bremen, Germany) and by Vitek II (BioMerieux, Nürtingen, Germany).

Data for all hedgehogs tested MRSA-positive are listed in Table 1. Four full genome sequences were obtained from three hedgehog isolates of CC599-MRSA-XI.

The first one originated from a road-killed hedgehog that was found in June 2014 [3] in the urban district Jena-Ost of the city of Jena in Thuringia, Germany (approximate coordinates 50°56'02"N : 11°35'53"E). A nasopharyngeal swab was taken. Gender, age and clinical data, beyond the observation of a massive and obviously fatal polytrauma, were not recorded due to the condition of the carcass. The isolate was assigned to CC599-MRSA-XI based on the identity of its array profile to an isolate from a human case [31] and on conventional MLST [51] and then it was earmarked for genome sequencing.

The second isolate originated from an adult, approximately 9 years old, female hedgehog “Anna” found in Jena that was brought to the local hedgehog rehabilitation centre in poor health in May 2024. CC599-MRSA-XI was isolated from homogenised ticks collected from this animal allowing the assumption that its condition was due to *S. aureus* bacteraemia. The hedgehog survived this episode but could not be released back into the wild due to age and overall poor health. It was kept nearly two years in the rehabilitation centre but finally euthanised. Because of divergent colony morphology, two subclones were eventually sequenced. One showed a normal morphology, the other one presented with autolysis and spontaneous plaque formation.

A third hedgehog isolate originated from a male hedgehog "Erik" that was submitted in summer 2025 in poor health and that showed skin lesions compatible with dermatophyte infection and staphylococcal superinfection leading to abscess formation and spine folliculitis. Indeed, *Trichophyton erinacei* was cultured. A nasal swab yielded CC599-MRSA-XI (which was sequenced) while CC130-MRSA-XI was cultured from a throat swab.

Additional hedgehog isolates CC599-MRSA-XI were identified by microarray but not yet sequenced (Table 1). Two isolates originated from a young, massively tick-infested male, "Rippi" that was kept in the rehabilitation centre for "aided" hibernation. Homogenised ticks were negative for *S. aureus*, but a nasopharyngeal swab and a stool sample were taken, and found positive, in March 2024 prior to release into the wild. "Oskar" was admitted in summer 2025, malnourished and parasitised. He recovered upon administration of anti-helminthic therapy (levamisole) plus co-trimoxazole and was released into the wild.

A fourth isolate was sequenced that was found in a screening swab of a human upon admission to a hospital in Bavaria. It differed from the hedgehog isolates in lacking some virulence markers as shown by microarray experiments (*tst1, sec, sel*; see below), and this observation prompted sequencing in order to analyse the integration site of the pathogenicity island with which these factors are associated. For another human isolate from Bavaria, contigs from an Illumina sequence were analysed because they included, unexpectedly, a CRISPR/*cas* operon (see below).

Microarray procedures

The primary characterisation of isolates, and identification as *mecC*-MRSA, was performed using a DNA-microarray-based assay (INTER-ARRAY, Bad Langensalza, Germany). Using this method, resistance genes (including *mecC* and *blaZ*-SCC*mec*XI) and virulence markers were detected and isolates were assigned to clonal complexes and strains. The microarrays, protocols and procedures as well as probe and primer sequences have previously been published [52-54]. In short, pure cultures were harvested and enzymatically lysed. Then, a multiplexed linear amplification with one

specific primer per target was employed to incorporate biotin-16-dUTP labels into the amplicons. After incubation and washing, these amplicons were hybridised to the probes on the array. Hybridisation were visualised by addition of streptavidin horseradish peroxidase and a dye that locally precipitated where the labelled amplicons were bound to the probes. Microarrays were photographed and analysed with a designated reader and software (INTER-ARRAY).

Nanopore sequencing

All bacterial strains were cultured at 37°C on Columbia blood agar (Becton Dickinson, Heidelberg, Germany). After overnight incubation, DNA was extracted using the Nucleospin DNA extraction protocol (Macherey Nagel, Düren, Germany), i.e., by bead-beating (BeadBug Homogenizer, Biozym, Germany), and enzymatic treatment with proteinase K and RNase. The DNA was finally eluted in nuclease-free water.

DNA was then prepared for sequencing using the barcoding kit 24 V14 (SQK-NBD114.24; Oxford Nanopore Technologies, Oxford, UK) following manufacturer's protocol. Prior to library preparation, DNA sample size selection was performed using AMPure beads (Beckman Coulter, Krefeld, Germany) at a 1:1 (v/v) ratio. Approximately 600 ng of DNA per sample, quantified with a Qubit 4 Fluorometer (Thermo Fisher Scientific, Waltham, MA, USA), was used for library preparation before loading onto an ONT flow cell (FLO-MIN114) equipped with R10.4.1 pores. For phage DNA, approximately 100 ng of input DNA were used.

Sequencing was performed on a MinION Mk1B device for 90 h, starting with at least 900 active pores and managed through MinKNOW software (v24.11.10). Base calling was carried out using the dorado basecaller (v1.0.2) with the model es_dna_r10.4.1_e8.2_400bps_sup@v5.0.0_bacterial-methylation, generating Fastq files containing 4,000 reads each. Barcode trimming was performed with dorado demux (v0.7.3) using the same model.

Quality-filtered reads were assembled into contigs using Flye software (v2.9.5; [55]). The resulting assemblies were polished in two stages: first, with four iterative rounds of Racon (v1.5.0; [56]) using

the parameters match 8, mismatch 6, gap 8, and a window length of 500; followed by a final polishing step with Medaka (v1.12.1; [57]) employing the model r1041_e82_400bps. The final corrected assemblies were subsequently used for downstream analyses

Phage induction and phage DNA isolation

Bacteriophages of isolates “Jena Ost” and “Anna” were induced as previously described [44, 50, 58-60]. In short, cultures were grown overnight in 2 × TY medium and cultivated at 37 °C until the mid-exponential growth phase. Then, mitomycin C (0.5 µg/mL) was added. Cultures were incubated at 30 °C until the OD600 decreased (see Table 2 for detailed information). The lysate supernatant was centrifuged at 4 °C and 3,000 × g, neutralized with 0.1 N NaOH and filtered through a 0.20 µm cellulose acetate filter (Sartorius, Göttingen, Germany). For phage DNA isolation, the filtrates were centrifuged again and then treated with 3 U/µL respectively 15,3 U/µL DNase I (Invitrogen, Carlsbad, USA) and 10 µg/mL RNase (Sigma-Aldrich Chemie GmbH, Taufkirchen, Germany) for 1 h at 37 °C and 550 rpm. Next, 20 mM respectively 10 mM EDTA (Carl Roth GmbH & Co KG, Karlsruhe, Germany) and 0.1% SDS (Carl Roth GmbH & Co KG, Karlsruhe, Germany) were added, and the mixture was incubated for 10 min at 65 °C to deactivate the DNase. Afterwards, 100 µg/mL proteinase K (EMBL, Heidelberg, Germany) was added and the mixture was incubated for 1 hour at 56 °C and 550 rpm. The DNA was isolated by phenol-chloroform extraction [61] and the concentration was determined with a Qubit 4 fluorometer (Table 2).

Phage detection by transmission electron microscopy (TEM)

Phage preparations were negatively stained as previously described [44, 50, 60, 62]. Briefly, 300 mesh copper grids filmed with formvar, coated with carbon, and hydrophilized by glow discharge were placed on 30 µl drops of phage preparations for 30 min. After washing with distilled water, they were placed for 1 min on a drop of 1% uranyl acetate. Grids were examined in a transmission electron microscope (Tecnai 12, FEI Deutschland GmbH, Dreieich, Germany). Phage particles were

microphotographed with a digital camera (TEMCAM FX416, TVIPS, Gauting, Germany) and measured using dedicated (TVIPS) software.

Results

Typing and core genomic markers

The isolate "Jena-Ost" had a MLST profile related to ST599, i.e., *arcC*-6, *aroE*-115, *glpF*-6, *gmk*-2, *pta*-7, *yqil*-5 and an undefined *tpi* allele. Its cgMLST profile was related to cgST5533, which is ST599, with 134 mismatches and 1,582 of 1,716 loci matching (92.2%). Its *spa* type was t5930 (RIDOM nomenclature, 04-17-25-16-16-23-34-34-34-34-34-50-17).

The isolates from "Hedgehog Anna" had the same MLST profile. The cgMLST profile was, again, related to cgST5533, with 140 mismatches and 1,576 out of 1,716 loci matching (91.8%). The *spa* type was undetermined with a repeat succession of 04-17-25-16-16-16-34-34-34-34-34-50-17.

The isolate from "Hedgehog Erik" had the same MLST profile. Its cgMLST profile was related to cgST5533, with 147 mismatches and 1569 of 1716 matching loci (91.4%) Its *spa* type was t5930.

The SCC*mec* XI element

The SCC*mec* XI element was, with regard to presence of genes, their orientation and allelic variants, essentially identical to the one in other *mecC*-MRSA/SCC*mec* XI sequences. A schematic diagram is provided in Figure 1, and a list of the genes including their positions based on the "Hedgehog Jena-Ost" sequence is provided in Table 2. For alignments, see Supplemental Files 2 and 3.

A comparison of the CC599 SCCmec XI sequences with other sequences (Table 2) showed that the SCCmec element is highly conserved, with a very limited number of single-nucleotide polymorphisms (Table 2). Apart from a 221 bp deletion in the lipase gene of CP155063, the number of SNPs per gene ranged between zero and two. The SNP count for all SCC*mec* XI ORFs together

(thus, excluding SCC*term*, direct repeats and *orfX*) ranges for the other sequences beside CP155063 from three to eleven (while for *orfX* alone, the number of SNPs ranges between five and nine).

Genomic islands

S. aureus has several large genomic islands (GIs), *i.e*., clusters of genes that are frequently, but not universally present and whose presence is linked to the clonal complex affiliation. Generally, two GIs are located directly downstream *orfX*/the SCC integration site, being separated by the ubiquitous genes *dusC* (encoding tRNA-dihydrouridine ligase-synthetase C), A6TXM6=DUF6007 (DUF6007 family protein, GenBank BA000033.2:(70,927..71,130)) and A6QD71 (putative protein/TfoX/Sxy family protein, BA000033.2:(71,179..71,475)). The first of them is commonly associated with exotoxin genes *seh* and ORF CM14, which, however, were absent in CC599. Instead, both islands contained a number of genes encoding "putative proteins" (see Supplemental File 3).

Interestingly, one human isolate from Regensburg/Bavaria had a CRISPR/*cas* operon located between the SCC*mec* element and the first genomic island. This operon was flanked by truncated transposase genes and it contained the same genes as the corresponding one in *S. argenteus* CC1850, strain MSHR1132 GenBank FR821777 (locus tags SAMSHR1132_00510 to _00600, see Supplemental File 3).

Another of these islands comprises leukocidin genes *lukD/E.* These were present in CC599, while the commonly associated enterotoxin gene cluster *egc* was absent. Instead, there were two poorly known superantigen-like genes (*seli2=sel26, selu2=sel27*). The same GI also harboured a hyaluronate lyase (*hysA*) gene, a type I restriction-modification system (*hsdS/M*), and seven genes encoding proteases (*splA/B/C* and four others).

Pathogenicity islands

Most notably, all hedgehog CC599 isolates tested by microarray, including the sequenced ones, harboured a *S. aureus* pathogenicity island (SaPI) carrying the toxic shock syndrome toxin gene (*tst1*) as well as enterotoxin C and L genes (*sec, sel*, see Supplemental File 4a). This SaPI integrated between *ktrB* (gene for the potassium uptake protein B, cgMLST SAUR2194) and *groL=groEL* (encoding a 60 kDa chaperonin, cgMLST SAUR2199), which is the same integration site as for the *tst1/sec/sel*-carrying SaPI known as nySa4 in human strains such as N315 (BA000018), Mu3 (AP009324), Mu50 (BA000017). Other animal strains such as RF122 (AJ938182) or ED133 (CP001996) also harbour a *tst1*-carrying SaPI (SaPIbov1) that, however, resides at another site while at their *ktrB/groL=groEL* site, other SaPIs integrate.

Compared to N315 (BA000018) and Mu50 (BA000017), the CC599 sequences lack the *ear* gene (encoding the "enterotoxin-linked ampicillin resistance protein", locus tags SAV2010, SA1818) which is neatly excised rather than replaced by a deviant allele or by, *e.g.,* a transposase gene.

Contrarily to N315 and Mu50, CC599 carried a probable transposase fragment and three "putative genes" (which are also known from BX571856: SAR2112 to SAR2115) directly upstream of the enterotoxin L gene. These genes were not identified in mitomycin-induced SaPIs (see below, and Supplemental File 4a). They were also present in the *tst1/sec/sel*-negative CC599-MRSA-XI isolate from a human patient from Regensburg (see Supplemental File 5). Thus, this gene cluster should rather be regarded as a separate but co-localised element than as part of the nySa4-like SaPI.

In addition, there was a second SaPI which carries a series of "genes of unknown function" (see Supplemental File 4b). It integrated between *rpsR* (cgMLST SAUR0366) and a genomic island comprising Q1XZL6 (putative protease/abortive phage infection protein, GenBank BA000033.2:(393,003..393,977) an integrase gene (*int-5-setC*, BA000033.2:(393,980..394,695), cgMLST SAUR0366) and *setC/selX* (staphylococcal enterotoxin-like toxin X, BA000033.2:(394,900..395,511)).

Prophages

There were three different prophages associated with the sequenced hedgehog isolates of CC599. The Illumina genome sequences of the human isolates were fragmented with the break lines being situated within the prophage sequences, and thus they were excluded from analyses.

First, all hedgehog CC599-MRSA-XI sequences harboured a 38,100 bp prophage consisting of 50 ORFs. It was integrated at an unusual integration site, between *glpD* and *miaA,* bisecting the *pldB*2 gene (cgMLST SAUR1306), see Supplemental File 5a. It did not harbour known enterotoxin, immune-evasion cluster or leukocidin genes. An assignment to genera based on the sequence was not unambiguously possible. Only two of its genes matched genes exclusively known from *Dubowvirus* sequences (*i.e.*, genes for "hypothetical proteins" corresponding phi-53-ORF114, AY954952:(698..838) and phi80alpha, DQ517338:(23,266..23,568)) while all its other genes occur either in different genera, or were found in phages/prophages which are not (yet) assigned to one of the five genera roughly corresponding to the former *Siphoviridae* family [63]. Similar prophage sequences were found in some but not all CC130-MRSA-XI (NZ_CP155063.1 carries a *pldB*2-integrating one, while NZ_CP155062.1 lacks it).

A second prophage was present only in the "Anna" isolates. This prophage bisected the former one, integrating into its major capsid protein gene. It harboured several genes known to be associated with Dubowviruses (see Supplemental File 5a).

Finally, "Anna" and "Erik" isolates harboured another *Dubowvirus* prophage that was absent from the "Jena-Ost" sequence. This phage integrated between the genomic island harbouring *lukD/E* and a cluster of tRNA genes (see Supplemental File 5b).

Transmission electron microscopy and phage sequencing

Sequencing of a mitomycin C phage preparation (Supplemental File 5a) of the Hedgehog "Jena-Ost" isolate revealed the presence of a genome corresponding to the *pldB2*-integrating prophage although no complete phage particles could be identified in TEM images. SaPI-associated genes (although neither *tst1* nor enterotoxin genes) were only found in non-circular contigs and associated with core genome markers, so that there was no evidence for an induction of the SaPI. In the phage preparation, numerous, long, convoluted, filaments with diameters between 5 nm and 10 nm (mean 8 nm, Figure 2 and Table 4) were seen. Images at higher magnification of filaments revealed a stack-disc appearance which is a common finding in tails of members of the former *Siphoviridae* family (Figure 2).

Phage preparations of both subclones of isolate "Hedgehog Anna", were investigated by TEM (Figure 3 and Table 4) and by nanopore sequencing. There were no differences noted between the subclones of that isolate. Sequencing showed the presence of a phage genome corresponding to the prophage situated next to *lukD/E* (Supplemental File 5b). Contrarily to "Jena-Ost", the phage genome genome corresponding to the *pldB2*-integrating prophage was not found, which might be explained by the fragmentation of that prophage by insertion of yet another prophage (see above). The latter one was also not found in the phage preparation. Sequencing also confirmed a present of the SaPI harbouring *tst1/sec/sel* (Supplemental File 4a). In TEM images of preparations of both subclones, isometric particles with large heads morphologically compatible with Dubowvirus predominated, but other particles with smaller heads were seen occasionally (Figure 3). This was compatible with the presence of sequences of a *Dubowvirus* and of a SaPI in the phage preparations (see Supplemental files 4a and 5b) assuming that phages and SaPIs differed in head size only.

Epidemiology in hedgehogs

Among 65 hedgehogs that were swabbed from 2024 to 2026 by the hedgehog rehabilitation team Jena/Saale-Holzland county, seven had *mecC*-MRSA. In addition, three cases of *mecC*-MRSA were

identified by random sampling in the years before (Table 1). Five hedgehogs carried CC599-MRSA-XI, four had CC130-MRSA-XI. One individual, “Erik”, had both MRSA strains. All *mecC*-MRSA-positive hedgehogs for which the age was noted were two years or older, both genders were affected, and individuals with clear signs of infection carried CC599-MRSA-XI.

Epidemiology in humans

Among 1,761 non-duplicate MRSA isolates collected and genotyped at the University Hospital in Dresden, Saxony, from 2000 to 2020, as part of screening or diagnostic procedures [54, 64], not a single one was CC599-MRSA-XI. Seven isolates were *mecC*-positive, but all belonged to CC130-MRSA-XI (0.40%).

Among 3,049 non-duplicate MRSA isolates collected in the Bavarian Regensburg University Hospital, 2010-2019, twelve (0.39%) were *mecC*-positive. Seven were CC130-MRSA-XI (0.23%) and five were assigned to CC599-MRSA-XI (0.16%). In addition to array-based genotyping, for two of these isolates conventional MLST was performed yielding sequence yielding ST599 (*arcC*-6, *aroE*-115, *glpF*-6, *gmk*-2, *pta*-7, *tpi*-32, *yqil*-5). For three isolates, *spa* typing was done, and all had the RIDOM *spa* type t1694 (04-17-25-16-16-23-34-50-17).

Among another 518 non-duplicate MRSA isolates collected and Illumina-sequenced in Regensburg University Hospital, 2020-2024, 11 were *mecC*-positive (2.12%). Five of them were assigned to CC130-MRSA-XI (0.96%) and six were CC599-MRSA-XI (1.16%). They all belonged to ST599, five had *spa* type t1694 (04-17-25-16-16-23-34-50-17) and one was *spa* type t232 (04-17-17). Two of these isolates lacked *tst1/sec/sel.* Two of this six CC599-MRSA-XI were associated with invasive processes, one was obtained from a mandibular abscess, the other one from a biopsy of a toe. The other isolates, as well as all CC130-MRSA-X, originated from nasal swabs taken for MRSA screening. Three of the eleven human isolates from Regensburg lacked *tst1*, *sec*, and *sel*; one harboured an additional CRISPR/*cas* operon as described above.

Discussion

The discovery of *mecC*-MRSA some fifteen years ago came as a major surprise. It required updates to screening procedures. Being found in humans, domestic and wildlife animals, *mecC*-MRSA carries significant implications to the "One Health" approach and its co-evolution with penicillin-producing dermatophytes represents another example for Darwinian evolution. It is another case where resistance to compounds used in medicine evolved in environmental bacteria unaffected by their medical use. Others are CTX-M beta-lactamases that apparently emerged in environmental enterobacteria, *Kluyvera spec.* [65], or the number of resistance genes found in a *Psychrobacter* preserved in 5,000-year-old cave ice [66]. They show that antibiotic compounds are a part of the living environment, and so is antibiotic resistance. It is therefore reasonable to expect that resistance genes towards supposedly new drugs already exist somewhere in nature and that they need only to be mobilized via mobile genetic elements to find their way into pathogenic bacteria.

CC599-MRSA-XI is a hedgehog-associated *mecC*-MRSA, and it is the least known, most poorly characterised one. Contrarily to most of the other *mecC*-MRSA lineages, no *mecC*-negative/methicillin-susceptible precursor strains are known. This might indicate that this was either an ancient lineage whose susceptible ancestors did not survive competition with beta-lactam-producing dermatophytes in a hedgehog environment, or that the lineage originated from some wild animal species whose *S. aureus* strains have not yet been sufficiently studied. As all *mecC*-MRSA, CC599 is interesting because it clearly demonstrates how evolution works. One microbe, the dermatophyte, evolved to produce antibiotic compounds to suppress the growth of potential competitors, which in turn evolve to become resistant by means of a horizontally transmissible mobile genetic element. Its transmissibility enabled other lineages to acquire this element and to enter the competition, so that by now at least six to seven lineages of *mecC*-MRSA (CC49, CC130, CC425, CC599, CC1943, CC2616 and possibly CC1, see Introduction) as well as additional lineages of *Mammaliicoccus spec.* (that also can carry *mecC*) compete with beta-lactam-producing dermatophytes for the skins and noses of hedgehogs. Other wildlife, livestock and humans might be

seen as collateral damage in this competition, albeit the more recently emerging use of beta-lactam antibiotics in veterinary and human medicine posed another, additional selective pressure that could also provide an advantage to *mecC*-MRSA over other, methicillin-susceptible, staphylococcal strains, resulting in an eventually increasing prevalence among non-hedgehog hosts.

Regarding geographic distribution, CC599-MRSA-XI is known to exist in England. Larsen et al. [34] mentioned two isolates from Berkshire, UK. The PubMLST database (accessed May 4th, 2026) lists seventeen isolates with ST599. Nine came from Germany, one from Switzerland and for seven, no country of isolation was stated. There was no information on host species or susceptibility test results. Other STs safely assignable to CC599 are ST2179, ST2508 and ST6459. For these, PubMLST lists (as May 4th, 2026) a total of six isolates. Two originated from England, two from Belgium, and for two, no country of origin was stated. Two isolates were cultured from humans, two from unnamed animals, for two, no data were provided. A study from Germany demonstrated a presence of CC599-MRSA-XI in clinical samples of dogs and cats from Bavaria, North Rhine-Westphalia and Hesse [14]. Based on the present work, it can be stated that CC599-MRSA-XI occur in wild hedgehogs in Thuringia, at a similar or possibly higher prevalence rate as CC130-MRSA-XI. It can be confirmed that it also occurs in Bavaria where it was found, increasingly common, in humans, but there the situation in hedgehogs is not yet studied.

CC599 causes skin and soft tissue infections in hedgehogs that might be superinfections of dermatophyte lesions. It can as well cause invasive disease. As described above, we isolated one from homogenised ticks collected from a sick hedgehog (“Anna”) likely indicating bacteraemia. While numbers are too low for statistical analyses, observations indicate that both, *Trichophyton erinacei* and *S. aureus/mecC*-MRSA, are more commonly found in adult or old individuals than in juvenile ones. If antibiotic treatment, of hedgehogs or of pets, is necessary, veterinary third-generation cephalosporins that are commonly used for pets cannot be expected to be effective. Paediatric co-trimoxazole can be considered as it is available as suspension and thus might be administered adapted to body weight.

The data from Regensburg might show an increase in the prevalence of *mecC*-MRSA in humans (from 0.39% in 2010-2019 to 2.12% in 2020-2024). Explanations for this apparent rise could be i) accidental, random fluctuation given that absolute numbers are still low, ii) a change in screening protocols or diagnostic procedures resulting in higher detection rates, iii) an increased transmission rate from hedgehogs to humans with, for instance, more people being possibly exposed to hedgehog carcasses and body fluids due to an increasing use of robotic lawn mowers, iv) an increase of the prevalence in hedgehog populations resulting in higher numbers of human cases even if modes of transmission remained unchanged or v) a real increase of the prevalence within the human population due to sustained transmission among humans.

The human isolates of CC599-MRSA-XI were mostly carriage isolates, but a pathogenic potential, as with all *S. aureus* strains, can be assumed, especially given the presence of the virulence factors *tst1, sec* and *sel* in most isolates. Thus, handling of hedgehogs, alive or dead, should be performed with some caution, possibly using protective gloves and hand disinfection is recommended afterwards. Contact to hedgehogs (or to robotic lawn mowers) should be regarded as risk factor for MRSA carriage, prompting for instance pre-operative screening and de-colonisation prior to surgical/orthopaedic procedures.

Analysing several human and hedgehog isolates, a certain variability within the CC599 lineage was noted. This affected MLST and *spa* types (see above) but also presence/absence of prophages, the absence of the *tst1/sec/sel* pathogenicity island from some isolates, or in an additional presence in one isolate of a CC1850-like CRISPR/*cas* operon localised downstream of SCC*mec.*

Open questions regarding *mecC*-MRSA in general and CC599-MRSA in particular to be solved in future study concern the clinical significance in humans and domestic animals/pets, temporal trends including a possibly increasing prevalence in humans, geographic distribution, the possible existence of *mecC*-negative/methicillin-susceptible ancestral strains, possibly in other host species, as well as of the role in pathogenicity and host specifity of the poorly characterised or unknown genes on the prophage and on the pathogenicity islands.

Declarations

Ethics approval and consent to participate

Not applicable. No experimentation on animals was performed. Animal isolates were collected in a non-invasive way in order to aid veterinary treatment and infection control. Human isolates were a by-product of routine diagnostic and screening procedures.

Availability of data and materials

All relevant information, including genome sequences, is present in the manuscript and in the Supplemental files. The complete sequences of the hedgehog isolates have been submitted to GenBank, accession numbers pending.

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

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Authors contributions

UP nursed and sampled the hedgehogs; ACP, BK, WSB, AS provided human isolates and epidemiological data used for the present study; SDB, CD, EM, MR, BK, SBV and ELT performed experiments and initial analyses; SM analysed the sequences, created Figure 1 and wrote the draft manuscript; CD and ELT wrote individual chapters of the text; RE reviewed the draft; UP, SDB,

SM, WSB and RE acquired funding. All authors read and approved the final version of the manuscript.

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Figures and Tables

Figure 1: Schematic representation of the SCC*mec* XI sequence of the CC599 hedgehog isolates. For details, see Table 3.

Figure 2: Filamentous structures from phage preparations of "Hedgehog Jena-Ost", transmission electron microscopic images of negative contrast preparations with uranyl acetate. Insert: Higher magnification of a filament revealing stack-disc appearance. Size bar = 100 nm, size bar insert = 50 nm.

Figure 3: Isometric particles from phage preparations of two subcultures of isolate "Hedgehog Anna", transmission electron microscopic images of negative contrast preparations with uranyl acetate. In preparations of both subclones, isometric particles with large heads (left) and with small heads (right) were present. This is compatible with the presence of sequences of a *Dubowvirus* and of a SaPI in the phage preparations. Presumed phages and SaPIs differed in head size only. Head shape, length and diameter of tails, and size and shape of baseplates were consistent, and there were no differences noted between the subclones of that isolate. Size bar = 100 nm.

Table 1: *mecC*-MRSA in studied hedgehogs.

Table 2: Phage induction experiments.

Table 3: Genes within the SCC*mec* XI element of the CC599-MRSA-XI, corresponding locus tags, coordinates (based on the Jena-Ost sequence) and number of single nucleotide polymorphisms (SNPs) compared to CC130-MRSA-XI: NZ_CP155062.1, NZ_CP155063.1, FR823292.1, CP028165.1 and to CC425-MRSA-XI: FR821779.1, LR134084.1.

Table 4: Measurements of phage and SaPI particles as observed in TEM.

Supplemental files

Supplemental File 1a: Genome sequence of the CC599-MRSA-XI isolate “Hedgehog Jena-Ost”.

Supplemental File 1b: Genome sequence of the CC599-MRSA-XI isolate “Hedgehog Anna I”.

Supplemental File 1c: Genome sequence of the CC599-MRSA-XI isolate “Hedgehog Anna II”.

Supplemental File 1d: Genome sequence of the CC599-MRSA-XI isolate “Hedgehog Erik”.

Supplemental File 2: SCC*mec* XI sequences and genes from this element.

Supplemental File 3: Partial contigs of the human isolate Regensburg 23U16538, including SCC*mec* XI, the CRISP/*cas* operon and the two genomic islands downstream, with “Hedgehog Jena-Ost” and “Hedgehog Anna I” sequences for comparison.

Supplemental File 4a: The *tst1/sec/sel* SaPI.

Supplemental File 4b: The second SaPI, localised downstream of *rpsR* [SAUR0366].

Supplemental File 5a: The *pldB2*-integrating prophage and the prophage-integrating prophage.

Supplemental File 5b: The prophage integrating between the genomic island harbouring *lukD/E* and a tRNA gene cluster, and exorcised phages.

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Figure 1: Schematic representation of the SCC*mec* XI sequence of the CC599 hedgehog isolates. For details, see Table 3.

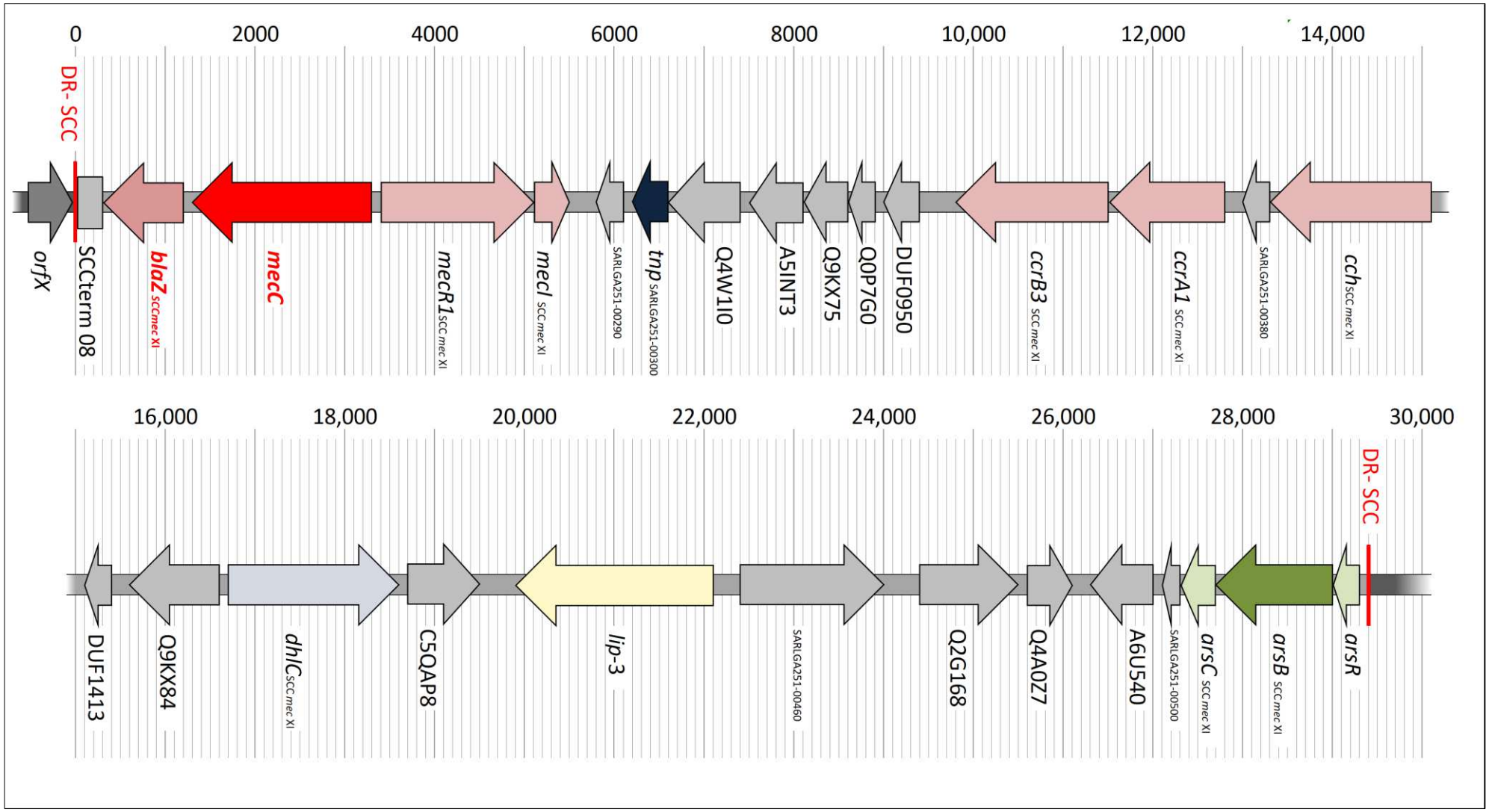


Figure 2: Filamentous structures from phage preparations of "Hedgehog Jena-Ost", transmission electron microscopic images of negative contrast preparations with uranyl acetate. Numerous, long, convoluted, filaments with diameters between 5 nm and 10 nm (mean 8 nm) were present. Insert: Higher magnification of a filament revealing stack-disc appearance. Size bar = 100 nm, size bar insert = 50 nm.

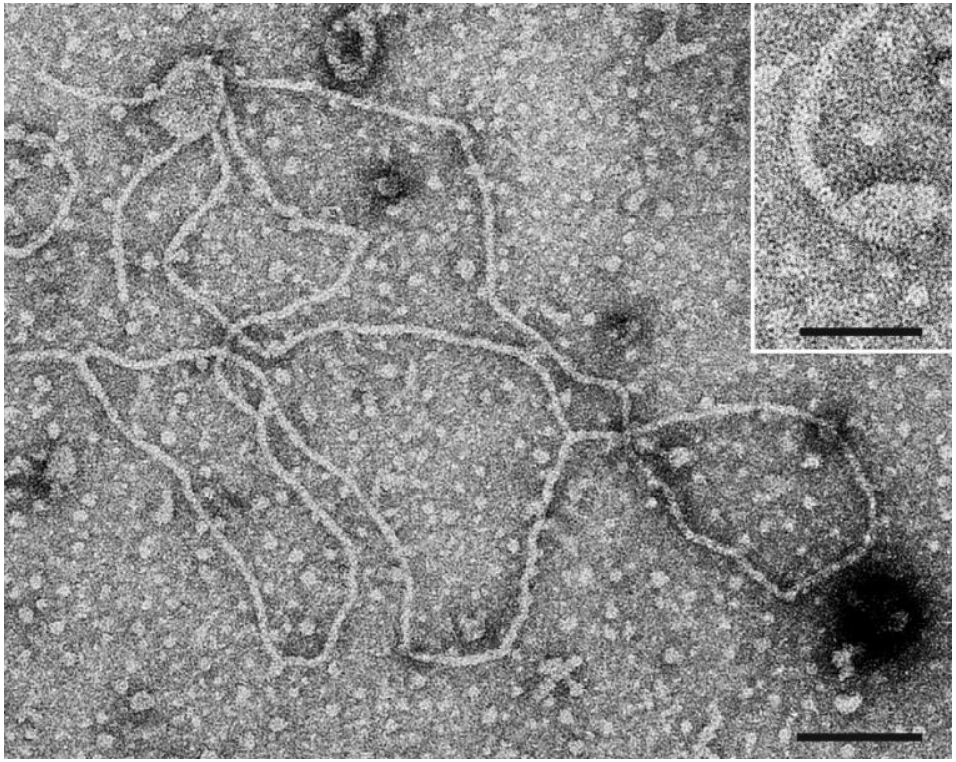


Figure 3: Isometric particles from phage preparations of two subcultures of isolate "Hedgehog Anna", transmission electron microscopic images of negative contrast preparations with uranyl acetate. In preparations of both subclones, isometric particles with large heads (left) and with small heads (right) were present. This is compatible with the presence of sequences of a *Dubowvirus* and of a SaPI in the phage preparations. Presumed phages and SaPIs differed in head size only. Head shape, length and diameter of tails, and size and shape of baseplates were consistent, and there were no differences noted between the subclones of that isolate. Size bar = 100 nm.

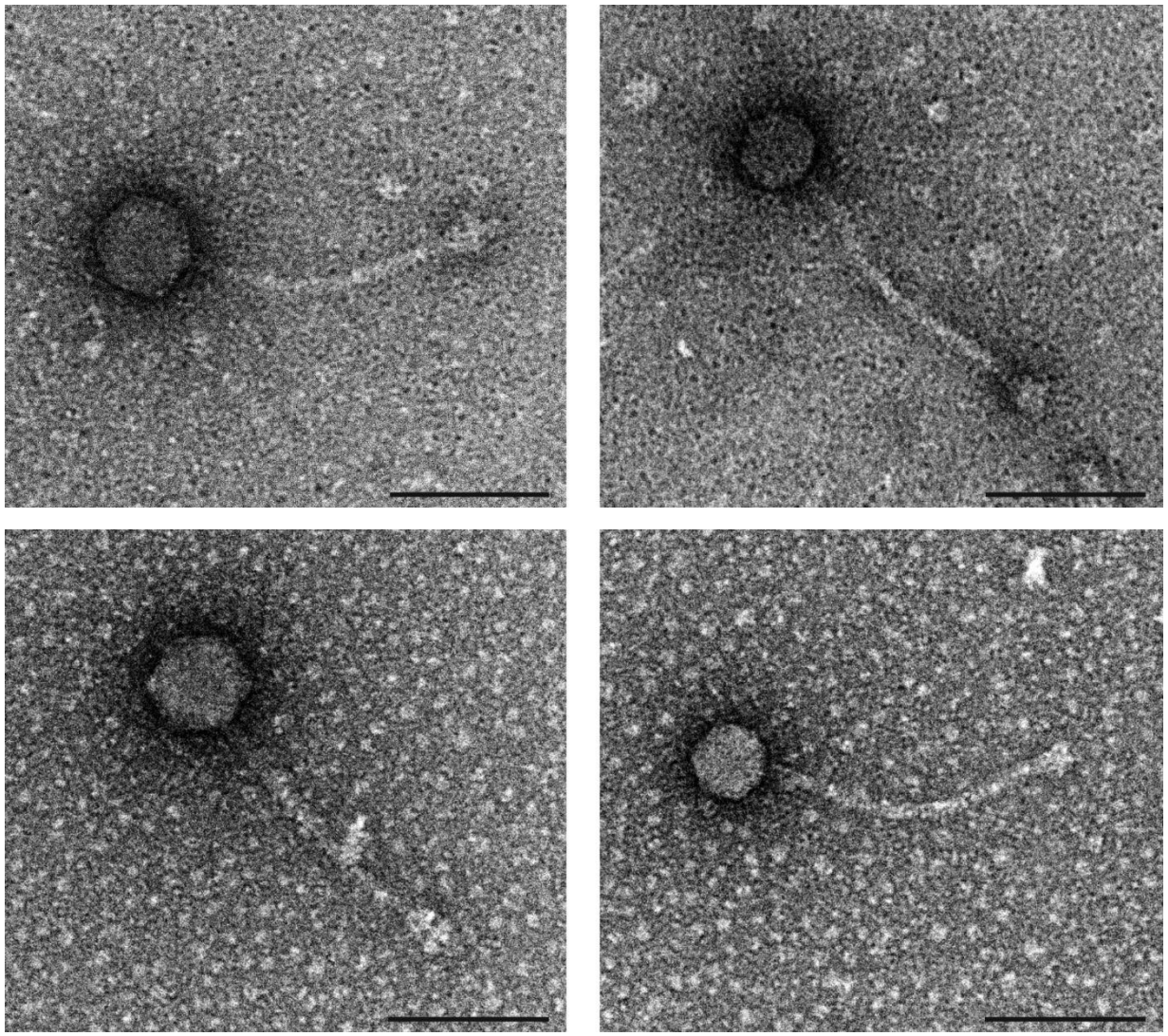


Table 1: *mecC*-MRSA in studied hedgehogs. Asterisks in the year´s column (*) indicate those that were identified when sampling systematically.

Hedgehog ID	Gender	Age	Body weight	Year	Underlying condition	Strain detected	Sample type	Method of characterisation
"Jena-Ost" (240048)	N/A	N/A	N/A	2014	Polytrauma/Road-kill	CC599-MRSA-XI	Nasopharyngeal swab	Microarray, nanopore WGS
"Anna" (99599, 99600)	F	> 5 yrs.	830 g	2024 *	Sepsis, multimorbid, old individual	CC599-MRSA-XI	Homogenised ticks	Microarray, nanopore WGS
"Rippi" (98495, 98496, 98497)	M	2-3 yrs.		2024 *	Too small and too thin to survive hibernation, massive infestation with ticks	CC599-MRSA-XI	Nasopharyngeal swabs and stool sample	Microarray
"Erik" (99616, 99617)*	M	adult	1350 g	2025 *	Skin lesions, leg injury, dermatophyte infection and staphylococcal superinfection	CC599-MRSA-XI, CC130-MRSA-XI	Nasal and throat swabs	Microarray, nanopore WGS (for the CC599 isolate)
"Oskar" (99615)	M	N/A	962 g	2025 *	Malnourished; helminthic infections	CC599-MRSA-XI	Throat swabs	Microarray
"Willow" (99784)	F	2-3 yrs.	890 g	2026 *	Facial injury by lawn mower	CC599-MRSA-XI	Wound swab	Microarray
"Jena-Cospeda" (289122)	N/A	juvenile	N/A	2016	Apparently healthy	CC130-MRSA-XI	Nasopharyngeal swab	Microarray
"Jena-Ost II" (305205)	N/A	N/A	N/A	2017	Polytrauma/Road-kill	CC130-MRSA-XI	Nasopharyngeal swab	Microarray
"Frieda" (98494)	F	N/A	849 g	2024 *	Healthy/Hibernating, parasitic infestation (*Capillaria aerophila, Crenosoma striatum*)	CC130-MRSA-XI	Rectal swab	Microarray
"Lucy" (99560)	F	N/A	645 g	2025 *	Healthy/Hibernating, too thin to survive	CC130-MRSA-XI	Pharyngeal swab	Microarray

Table 2: Phage induction experiments.

	"Jena-Ost"	**"Anna 1"**	**"Anna 2"**
Time of induction after the start of cultivation	150 min	150 min	150 min
OD at the time of induction	0.79	0.76	0.75
Time of of cultivation	420 min	420 min	270 min
Δ OD	0.10	0.20	0.20
Concentration of phage DNA	3.86 ng/µl	5.1 ng/µl	5.4 ng/µl

Table 3: Genes within the SCC*mec* XI element of the CC599-MRSA-XI, corresponding locus tags, coordinates (based on the Jena-Ost sequence) and number of single nucleotide polymorphisms (SNPs) compared to CC130-MRSA-XI: NZ_CP155062.1, NZ_CP155063.1, FR823292.1, CP028165.1 and to CC425-MRSA-XI: FR821779.1, LR134084.1.

Gene ID	**Corresponding locus tags in M10/0061 (FR823292.1) and LGA251 (FR821779.1)**	**Explanation / Gene product**	**Start**	**End**	**Length**	**Orientation**	**SNPs *vs.* CC130 CP155062**	**SNPs *vs.* CC130 CP155063**	**SNPs *vs.* CC130 FR823292**	**SNPs *vs.* CC130 CP028165**	**SNPs *vs.* CC425 FR821779**	**SNPs *vs.* CC425 LR134084**
orfX	FR823292-ORF_100 SARLGA251_00240	23S rRNA Pseudouridine(1915)-N(3))-methyltransferase RlmH	35,349	35,828	480	forward	9	9	9	9	5	5
DR_SCC	N/A	Direct repeat of SCC	35,810	35,828	19	N/A	0	0	0	0	0	0
SCC*term* 08	N/A	Terminus of SCC towards *orfX*	35,829	36,071	243	N/A	0	0	0	0	0	0
blaZ-SCC*mec*XI	FR823292-ORF_101 SARLGA251_00250	Beta-lactamase gene associated with *mecC*/SCC*mec* XI	36,144	36,995	852	reverse compl.	1	1	1	1	1	1
mecC	FR823292-ORF_102 SARLGA251_00260	Alternative penicillin binding protein 2a, *mecC* from SCC*mec* XI	37,089	39,086	1998	reverse compl.	0	0	1	0	0	1
mecR1-SCC*mec*XI	FR823292-ORF_103 SARLGA251_00270	Methicillin resistance protein MecR1	39,187	40,941	1755	forward	0	0	0	0	0	1
mecI-SCC*mec*XI	FR823292-ORF_104 SARLGA251_00280	Methicillin resistance regulatory protein	40,938	41,312	375	forward	0	0	0	1	0	0
-	FR823292-ORF_105 SARLGA251_00290	Putative membrane protein	41,568	41,930	363	reverse compl.	0	0	0	0	0	0
tnp	FR823292-ORF_106 SARLGA251_00300	Putative exported protein/transposase	41,890	42,357	468	reverse compl.	0	0	0	0	0	0
Q4W1I0	FR823292-ORF_107 SARLGA251_00310	Putative DNA binding regulator	42,374	43,258	885	reverse compl.	0	0	0	0	0	0
A5INT3-SCC*mec*XI	FR823292-ORF_108 SARLGA251_00320	Putative protein/RadC domain-containing protein	43,456	43,875	420	reverse compl.	0	0	0	0	1	1
Q9KX75-SCC*mec*-XI	FR823292-ORF_109 SARLGA251_00330	Putative protein/DUF1643 domain-containing protein	43,896	44,402	507	reverse compl.	0	0	0	0	0	0
Q0P7G0	FR823292-ORF_110 SARLGA251_00340	Putative protein	44,418	44,729	312	reverse compl.	0	0	0	0	0	0
DUF0950=Q93IE0	FR823292-ORF_111 SARLGA251_00350	Staphylococcal protein of uncharacterised function (DUF950)	44,825	45,163	339	reverse compl.	0	0	0	0	0	0
ccrB-3-SCC*mec*XI	FR823292-ORF_112 SARLGA251_00360	Cassette chromosome recombinase B, type 3	45,638	47,266	1629	reverse compl.	1	1	1	0	0	0
ccrA-1	FR823292-ORF_113 SARLGA251_00370	Cassette chromosome recombinase A, type 1	47,287	48,636	1350	reverse compl.	0	1	0	0	0	0
-	N/A SARLGA251_00380	Putative protein	48,814	49,071	258	reverse compl.	0	0	0	0	1	1
cch-SCC*mec*XI	FR823292-ORF_114 SARLGA251_00390	Putative membrane protein/putative DNA helicase	49,139	50,932	1794	reverse compl.	0	0	1	0	1	1
DUF1413	FR823292-ORF_115 SARLGA251_00400	Putative protein associated with *cch,* single-stranded DNA-binding protein	50,932	51,225	294	reverse compl.	0	0	0	0	0	0
Q9KX84	FR823292-ORF_116 SARLGA251_00410	Putative protein	51,408	52,412	1005	reverse compl.	1	1	1	0	1	1
dhlC-SCC*mec*XI	FR823292-ORF_117 SARLGA251_00420	Putative protein/putative DNA helicase	52,519	54,450	1932	forward	0	0	0	0	0	0

Gene ID	**Corresponding locus tags in M10/0061 (FR823292.1) and LGA251 (FR821779.1)**	**Explanation / Gene product**	**Start**	**End**	**Length**	**Orientation**	**SNPs *vs.* CC130 CP155062**	**SNPs *vs.* CC130 CP155063**	**SNPs *vs.* CC130 FR823292**	**SNPs *vs.* CC130 CP028165**	**SNPs *vs.* CC425 FR821779**	**SNPs *vs.* CC425 LR134084**
C5QAP8-SCC*mec*XI	FR823292-ORF_118 SARLGA251_00430	Putative membrane protein	54,541	55,323	783	forward	0	0	0	0	0	0
lip-SCC*mec*XI	FR823292-ORF_119 SARLGA251_00440+450	Lipase gene associated with SCC*mec* XI	55,736	57,901	2166	reverse compl.	0	221	0	0	2	2
-	FR823292-ORF_120 SARLGA251_00460	Putative protein/FAD-binding dehydrogenase	58,200	59,849	1650	forward	0	0	0	0	1	1
Q2G168	FR823292-ORF_121 SARLGA251_00470	ABC transporter, transmembrane permease	60,215	61,264	1050	forward	0	0	0	0	0	0
Q4A0Z7	FR823292-ORF_122 SARLGA251_00480	ABC transporter, ATPase	61,282	61,950	669	forward	1	1	1	1	1	1
A6U540-SCC*mec*XI	FR823292-ORF_123 SARLGA251_00490	Putative flavin reductase associated with SCC*mec* XI	62,091	62,771	681	reverse compl.	0	1	0	0	0	0
-	FR823292-ORF_124 SARLGA251_00500	Major facilitator superfamily protein/DUF1837 superfamily protein	62,892	63,062	171	reverse compl.	0	0	0	0	0	0
arsC-SCC*mec*XI	FR823292-ORF_125 SARLGA251_00510	Arsenate reductase, SCC*mec* XI-borne/*mecC*-associated gene	63,099	63,491	393	reverse compl.	0	0	0	0	0	0
arsB-SCC*mec*XI	FR823292-ORF_126 SARLGA251_00520	Arsenical pump membrane protein, plasmid-borne gene	63,509	64,798	1290	reverse compl.	1	2	1	0	0	0
arsR-SCC*mec*XI	FR823292-ORF_127 SARLGA251_00530	Repressor of arsenic resistance operon	64,798	65,112	315	reverse compl.	0	0	0	0	0	0
DR_SCC	N/A	Direct repeat of SCC	65,232	65,250	19	N/A	0	0	0	0	2	2

Table 4: Measurements of phage and SaPI particles as observed in TEM (n, number of measured particles; m, mean; SD, standard deviation; all measurements in nm).

Hedgehog/ Isolate ID	**n**	**Head length, m±SD**	**Head length, range**	**Head diameter, m±SD**	**Head diameter, range**	**Tail length, m±SD**	**Tail length, range**	**Tail diameter, m±SD**	**Tail diameter, range**	**Baseplate**	**Morphology consistent with**
„Jena-Ost“	52	N/A	N/A	N/A	N/A	135±46	50-254	8±1	5-10	N/A	N/A
„Anna 1“	22	61±2	58-65	61±2	57-66	177±10	151-203	10±1	8-13	22 to 38 x 20 to 33	*Dubowvirus*
	2	46; 44	-	47 and 49	-	184 and 162	-	9 and 10	-	21 x 22	SaPI
„Anna 2“	10	60±3	53-64	61±2	58-63	173±12	162-190	10±1	9-12	25 to 36 x 19 to 30	*Dubowvirus*
	5	48±5	41-54	49±5	41-54	150		9±0		22 x 22	SaPI

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