Diversity of staphylococcal cassette chromosome in coagulase-negative staphylococci from animal sources

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Abstract

Aims: To type the staphylococcal cassette chromosome (SCC) in coagulase-negative staphylococci (CoNS) from animal sources.

Methods and Results: A total of 92 CoNS isolates recovered from farm animals was analysed. The top three staphylococcal species were Staphylococcus lentus (34), S. sciuri (31), and S. xylosus (13). The presence of the cassette chromosome recombinase (ccr) genes ccrA1, ccrB1, ccrA2, ccrB2, ccrA3, ccrB3 and ccrC, the mec regulatory genes mecI and mecR1, and Tn554 was used to differentiate the SCC. A total of 60 of the 92 isolates were methicillin resistant. Among the 60 methicillin-resistant Staphylococcus spp. isolates, SCCmec (mecA-carrying SCC) types I, III, IV and V were identified in 24 isolates based on the combinations of the ccr genes and the mec regulatory genes, with type III being predominant. The single S. epidermidis carried SCCmec type IV. SCC type III was also identified in two of 32 methicillin-susceptible isolates. Identical SCCmec types were present in different species of CoNS. Pulsed-field gel electrophoresis (PFGE) generated 64 patterns out of 81 PFGE typeable isolates. Indistinguishable clones were detected in animals from different farms.

Conclusions: Heterogeneous SCC existed in CoNS of diverse genetic background. Both clonal transmission of methicillin-resistant CoNS and horizontal transfer of SCCmec occurred in the animal production environment.

Significance and Impact of the Study: This study adds to our knowledge of SCCmec type and the diversity of SCC in CoNS.

Introduction

Coagulase-negative staphylococci (CoNS) can cause severe animal diseases, such as suppurative disease, mastitis, arthritis, and urinary tract infection (Lee 2003). CoNS were also the number one bacterial agent in monomicrobial nosocomial bloodstream infections in the US, followed by Staphylococcus aureus and enterococci (Rice 2006). Transmission of staphylococci between animals (cows, pigs, horses, and dogs) and humans has been reported (Juhasz-Kaszanyitzky et al. 2007), suggesting that staphylococci in animal species may serve as a reservoir for human infections.

The significance of CoNS is also reflected by the potential contribution of methicillin-resistant CoNS to the emergence of MRSA by transmitting mecA to methicillin-susceptible S. aureus (Yasuda et al. 2000; Hanssen and Ericson Sollid 2006). The gene mecA confers methicillin resistance by encoding a penicillin-binding protein (PBP2a) and is located on a mobile genetic element called staphylococcal cassette chromosome (SCC). The reservoir of these mecA-carrying SCC (SCCmec) is likely to be larger in CoNS than that in S. aureus as more than 70% of CoNS are methicillin resistant among human clinical isolates in the US, whereas only 34-2% of S. aureus are methicillin resistant (Diekema et al. 2001). Although scientific evidence supports horizontal transfer of mecA, the transfer mechanism has yet to be discovered. Analysis on SCC, the vehicle of mecA, may provide valuable information on the genetic basis on which mecA transfers among
staphylococci. There are currently six major SCCmec types (I, II, III, IV, V and IV) and several SCCmec subtypes (Hanssen and Sollid 2007) based on the combination of the cassette chromosome recombinase (ccr) gene complexes and mecA regulatory genes, mecI and mecR1. In addition, new SCCmec types or elements are being discovered continuously around the world (Berglund et al. 2008; Descloux et al. 2008). Staphylococcus epidermidis SCCmec type IV has been suggested to be responsible for the conversion of commensal S. aureus to MRSA (Hiramatsu et al. 2001).

Methicillin-resistant CoNS have been recovered from animals. van Duijkeren et al. (2004) identified methicillin resistance in four of 100 CoNS and none of 200 coagulase-positive staphylococci from various animal species. Fifteen of 56 (27%) CoNS isolated from healthy horses in Japan were methicillin resistant (Yasuda et al. 2000). In another study investigating staphylococci from Cope’s grey treefrogs, the animals often used in elementary and secondary science classrooms, 59% of the CoNS were methicillin resistant (Slaughter et al. 2001).

Despite the recovery of the resistance phenotype in the above mentioned studies, most work on methicillin-resistant staphylococci has focused on MRSA and much less data are available on CoNS and the distribution of SCCmec types in CoNS. The current study was aimed to compare the molecular subtypes and the compositions of SCC in 92 CoNS isolates from animal origin to improve our understanding on methicillin-resistant CoNS as a potential source of human infections and reservoir of methicillin resistance genes.

### Materials and methods

#### Sample collection and strain identification

On three spate days during the summer of 2006, cotton-tipped applicators were used to swab the oropharyngeal cavity and rectum/cloacal of a variety of agricultural animals (Table 1) presented for sale at a livestock auction in northeastern Ohio. Animals tested represented a convenience sample of animals available on any particular day. Swabs were incubated in Tryptic Soy Broth (TSB; Difco, Detroit, MI, USA) supplemented with 10% NaCl for 20 h at 35°C. The enrichments were struck to Mannitol Salt Agar (MSA, Difco, Detroit, MI, USA) supplemented with 10% NaCl for 20 h. The enrichments were then streaked on Cefoxitin-Mannitol Salt Agar (C176 Agar, Difco, Detroit, MI, USA) for isolation of methicillin-resistant staphylococci. Strain confirmation was performed by Gram staining (Gram-positive cocci) and catalase tests (positive). Coagulase-negative staphylococci were identified by tube coagulase tests (BD Diagnostics, Sparks, MD, USA) and API-Staph biochemical tests (bioMerieux, Durham, NC, USA). Isolates recovered were amplified by overnight in enrichment in Brain Heart Infusion broth (BHI, Difco, Detroit, MI, USA) and banked at −70°C, with 30% buffered glycerol until further analysed.

#### Antimicrobial susceptibility tests

The Minimal Inhibitory Concentrations (MICs) of cefoxitin were determined by an agar dilution method (Lee 2003). Cefoxitin (Sigma, St Louis, MO, USA) at concentrations from 0.5 to 128 μg ml⁻¹ was added to Mueller-Hinton agar (Difco, Detroit, MI, USA) supplemented with 10% NaCl.
with 2% of NaCl. An inoculum of 10^4 Colony Forming Unit (CFU) was spotted on the Mueller–Hinton Agar followed by incubation at 35°C for 24 h. The MIC used to predict mecA presence was 8 μg ml\(^{-1}\) (Swenson and Tenover 2005). S. aureus ATCC29213 was used as quality control organism.

SCC typing and amplification of mecA, IS431 and Tn554

SCC typing was performed as previously described (Van-

nuffel et al. 1995; Hansen et al. 2004; Deurenberg et al.

2005). Cassette chromosome recombinase genes (ccrA1,

ccrB1, ccrA2, ccrB2, ccrA3, ccrB3, and ccrC) and mec regulatory genes (mecI, mecR1-A for the membrane-spanning part of mecR1, and mecR1-B for the penicillin-binding part of mecR1) were amplified by PCR. Presence of mecA, IS431 and Tn554 was examined by target-specific PCR. DNA template was prepared by a boiling method as described previously (Hansen et al. 2004). The combinations of ccr types and classes of mec gene complexes were used to differentiate the SCCmec types among isolates. The classification scheme was as followed: SCCmec type I (ccrA1, ccrB1, mecR1-A), type II (ccrA2, ccrB2, mecI, mecR1-A, mecR1-B, Tn554), type III (ccrA3, ccrB3, mecI, mecR1-A, mecR1-B, Tn554), type IV (ccrA2, ccrB2, mecR1-A), and type V (ccrC, mecR1-A). The SCCmec types were determined solely on the ccr types when the combination of ccr types, mec gene complex, and Tn554 failed to designate the SCCmec types (Deurenberg et al. 2005). No SCCmec types were assigned when none of the ccr genes was amplified by PCR.

Pulsed-field gel electrophoresis

Pulsed-field gel electrophoresis (PFGE) was carried out to
distinguish CoNS at the genomic level using a previously
described method (McDougal et al. 2003) with a few
modifications. Briefly, genomic DNA was prepared by
mixing 300 μl of standardized cell suspension in TE buf-
derer (10 mmol l\(^{-1}\) Tris–HCl and 1 mmol l\(^{-1}\) EDTA, pH
8.0), 4 μl of 1 mg ml\(^{-1}\) lysostaphin solution (Sigma), and
300 μl of melted 1.5% Seakem Gold agarose. Sample
plugs were then incubated in EC buffer (6 mmol l\(^{-1}\)
Tris–HCl, 1 mol l\(^{-1}\) NaCl, 100 mmol l\(^{-1}\) EDTA, 0.5% Brij-58, 0.2% Sodium deoxycholate, and 0.5% Sodium
laurylsarcosine) supplemented with lysozyme (Sigma) at
a final concentration of 1 mg ml\(^{-1}\) at 37°C for 4 h, fol-
lowed by an overnight cell lysis at 54°C with
0.15 mg ml\(^{-1}\) of proteinase K (Sigma). Plugs were
digested with 20 U of Sma I (New England Biolabs, Be-
verly, MA, USA) at 25°C overnight. Electrophoresis was
carried out on a CHEF-DR III apparatus (Bio-Rad Labo-
ratories, Hercules, CA, USA) using the following parame-
ters: initial switch time, 5 s; final switch time, 40 s; run
time, 20 h; angle, 120; gradient, 6 V cm\(^{-1}\); temperature,
14°C; ramping factor, linear. Staphylococcus aureus
NCTC8325 was used as the reference standard. The PFGE
patterns were compared using the BioNUMERICS software
program (ver. 5.0; Applied Maths, Austin, TX, USA).
Clustering was performed by using the Dice similarity
coefficient and the unweighed pair group method with
arithmetic means (UPGMA), with 1.5% of position
tolerance and 1% optimization.

Results

Diverse CoNS species in animals in northeastern Ohio

A total of 92 CoNS were isolated (Table 1). Most animals
tested yielded CoNS from either the respiratory or the
gastrointestinal tract. Nine staphylococcal species were
identified, with S. lentus (n = 34), S. sciuri (n = 31), and
S. xylosus (n = 13) the top three recovered in this study.
More than 72% (67 of 92) of the isolates were recovered
from cattle, sheep, and goats. Each of these three animals
was reservoir of at least four staphylococcal species.
S. lentus was the most frequently isolated species from
sheep, pigs and chicken, whereas S. sciuri showed the
highest isolation rate from cattle, goats and duck. Goats,
pigs, duck, chicken, and turkey were also hosts of more
than two staphylococcal species. The single isolates from
a goose and a horse belonged to the species S. xylosus
(Table 1).

Isolation of methicillin-resistant coagulase-negative
staphylococci (MR-CoNS) from animals

Among the 92 CoNS isolates, 60 were mecA positive and
therefore considered as methicillin resistant. They were
recovered from eight animal species, except for horse.
Most methicillin-resistant isolates (45 of 60) were from
cattle, sheep, and goats. Of the 60 mecA-positive isolates,
40 demonstrated MICs of equal to or higher than
8 μg ml\(^{-1}\) of cefoxitin. There was no clear distinction
among animals in terms of presence or absence of the
meca gene. However, a higher rate of mecA detection was
observed in isolates from sheep, goats, and pigs, and all
five isolates from chicken samples carried mecA (Table 1).
Five of six CoNS from duck failed to show mecA
amplicons.

High prevalence of IS431 in MR-CoNS

A much higher detection rate of IS431 was observed in
meca-positive CoNS compared to the mecA-negative
isolates, with 90% vs 31% (54 of 60 and 10 of 32,
respectively). Six mecA-positive isolates lacked IS431. These isolates were three S. sciuri, one S. haemolyticus, one S. lentus, and one S. epidermidis (IDs 3, 50, 69, 86, 87, and 88 in Fig. 1). The 10 IS431-positive CoNS without mecA were from various animals and included four S. lentus, three S. sciuri, two S. haemolyticus, and one S. xylosus.

Heterogeneity of SCC in CoNS

SCCmec or SCC type III was identified in 21 isolates, with 19 being mecA positive (Table 2). The 21 isolates included 11 S. lentus, seven S. sciuri, and three S. xylosus, among which one S. lentus and one S. sciuri were mecA-negative. Two S. sciuri from cattle contained SCCmec type I and they shared identical gene profiles (Table 2). Another two S. sciuri from cattle belonged to SCCmec type V as ccrC was detected from both isolates, although one lacked Tn554. The single S. epidermidis contained mecA and the SCCmec belonged to type IV. A total of 42 isolates did not have any ccr or mec regulatory genes. The remaining 24 isolates had no ccr genes but a large variety of the mec regulatory gene complexes was observed among these isolates.

ccrA3 and ccrB3 were the most common ccr genes detected (Table 2). Among mecA-positive isolates, eight harbored prototypic type III SCC, demonstrating positive PCR reactions on ccrA3, ccrB3, all the mec regulatory genes, Tn554, and mecA. These isolates included four S. lentus, two S. sciuri, and two S. xylosus, which were recovered from sheep, cattle, and goats. Another eight isolates showing similar gene profiles, with the only difference in lacking Tn554, were also designated as SCCmec type III as both ccrA3 and ccrB3 were detected. The isolates were recovered from cattle, sheep, goats, and pigs, including four S. lentus, three S. sciuri, and one S. xylosus. Likewise, various combinations of the mec regulatory genes and Tn554 were identified in the remaining three isolates belonging to SCCmec type III. mecA was the only gene detected in 17 mecA-positive CoNS. In the remaining 19 ccr-negative isolates, various rearrangements of the mec regulatory genes were observed, in addition to mecA. On the other hand, none of the mec regulatory genes was detected in two isolates with ccrA3 and ccrB3 amplified.

In the 32 mecA-negative isolates, type III SCC was identified in one S. lentus from goat and one S. sciuri from cattle. The S. lentus isolate carried ccrA3, ccrB3, mecI, mecR1, and Tn554, whereas Tn554 was missing in the S. sciuri isolate. No genes were detected in the vast majority of the mecA-negative CoNS (25 of 32). Although no mecA was identified, all or some of the mec regulatory genes were detected in five isolates.

CoNS of diverse genetic background recovered from animals

PFGE generated 64 patterns out of 81 isolates. The dendrogram is shown in Fig. 1. Eleven CoNS were non-typeable by PFGE. Overall, the PFGE patterns distributed randomly among isolates in terms of staphylococcal species, animal origins, mecA presence, and SCCmec types. Two isolates carrying SCCmec type I (IDs 15 and 16) shared identical PFGE patterns. Most of the 20 SCCmec type III isolates that were typeable by PFGE were clustered into four clonal groups, with the similarity index ranging from 82.3% to 88.00%. The two SCCmec type V isolates (IDs 10 and 14) demonstrated a distant relationship at the genomic level. The single S. epidermidis (SCCmec type IV, ID 88) showed a unique pattern compared to all other subtypes. Three groups of isolates carrying no ccr genes were clustered at the top, middle, and bottom of the dendrogram, respectively.

Two S. sciuri from cattle (15 and 16), two S. sciuri from duck (83 and 96), and two S. lentus from sheep (40 and 51), were identical clones based on PFGE and SCC typing. Most isolates sharing identical PFGE patterns were from the same staphylococcal species, however, some isolates with indistinguishable PFGE patterns belonged to different species. For example, isolates 64 and 65 were S. xylosus and S. lentus, respectively, but they were indistinguishable by PFGE. Another difference between the two isolates was the absence of Tn554 from 65 (data not shown). Isolate 62, S. lentus, shared identical PFGE pattern with four other S. xylosus isolates from goats and cattle. Isolates 86 (S. haemolyticus) and 89 (S. lentus) demonstrated indistinguishable PFGE subtypes, so did isolates 5 (S. sciuri) and 6 (S. xylosus). Some isolates with identical PFGE patterns and from the same staphylococcal species (74 and 80, 54 and 72, 68 and 77, 30, 31, 45 and 48, 34 and 39) were differentiated by either mecA presence, the ccr genes, or the mec regulatory complex (data not shown).

Discussion

Methicillin resistance in staphylococci is a great concern to public health and animal welfare. Most studies on mecA and its vector, SCC, have focused on MRSA from human clinical samples, whereas less research effort has been put on CoNS, a group of staphylococci that are believed to have a larger pool of mecA and SCC than their coagulase-positive counterparts (Hanssen and Sollid 2007). This study reports heterogeneity of SCCmec types present in a diverse population of CoNS from farm animals. Both mecA-positive and -negative CoNS are carriers of previously reported SCCmec types. Horizontal transfer
Figure 1 Dendrogram of the 81 CoNS isolates from animals in this study.

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of mecA and SCC occurs in CoNS from farm animals, which may pose potential threat to humans. Isolation of multiple staphylococcal species and recovery of methicillin-resistant CoNS from most animals indicate a large reservoir of CoNS and mecA in animals, which is in agreement with previous studies. Yasuda et al. (2000) reported six different species of CoNS from healthy horses in Japan. mecA-positive CoNS were isolated from 45 horses (22.5%) in the Netherlands (Busscher et al. 2006). Another study recovered methillin-resistant S. epidermidis and S. xylosus from milk of dairy ewes (Burriel 1997), suggesting a potential risk from consuming foods of animal origin. Our study demonstrated mecA-positive CoNS carriage among a variety of

![Figure 1](http://example.com/image1.png)

**Figure 1 (Continued).**
animals, including sheep, goats, pigs, and chickens. Variations among animal species, sampling sizes, as well as agricultural practices may lead to difference in known and unknown factors altering exposure doses and frequency, and also providing differential factors responsible for antimicrobial resistance selection. The low agreement observed in this study between mecA detection by PCR and cefoxitin MIC test to predict methicillin resistance in CoNS is not unexpected compared to previous investigations where low sensitivities of phenotypic methods were reported when testing CoNS. This could be due to the fact that heterogeneous expression of mecA is more common in CoNS than that in S. aureus (Swenson and Tenover 2005; Stepanovic et al. 2006; Join-Lambert et al. 2007). Low specificities of phenotypic methods have also been reported in previous studies (Swenson and Tenover 2005; Stepanovic et al. 2006; Join-Lambert et al. 2007) as demonstrated by non-mecA-carrying CoNS with resistance phenotypes, which were as well observed in our study (data not shown). All these findings suggest that mecA detection by PCR is still the best tool to identify methicillin-resistant staphylococci (Swenson and Tenover 2005) and use of cefoxitin MIC test as a predictor of resistance other than methicillin resistance due to the invertase-resolvase activity of the ccr genes. The detection of the mec regulatory genes in five mecA-negative CoNS in this study is interesting as one would assume that the mec regulatory genes always coexist with mecA. Indeed, researchers have reported mecA-positive CoNS with no mec regulatory genes (Ibrahem et al. 2009) as well as mecA-negative Staphylococci carrying part of mecI (Shore et al. 2008). This, together with our findings, suggests that the mecA complex may undergo significant genetic exchange during its evolution and partial deletion in the mec regulatory genes may occur before mecA transfers.

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<th>ccr genes</th>
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<td>A3, B3</td>
<td>mecI, mecRI-A</td>
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*+, all genes, mecI, mecRI-A, and mecRI-B are present; –, all genes are absent; var., various rearrangements in mecI and/or mecRI-A and/or mecRI-B.
†, no SCC/SCCmec types designated based on the ccr and mec gene complex.

Diversity of SCC in CoNS

Recurrence of diverse SCCmec types in CoNS in this study indicates a large reservoir of SCCmec in methicillin-resistant CoNS from animal origin. Dominance of SCCmec type III in the typeable mecA-positive CoNS is in accordance with previous finding by Hanssen et al. (2004), who, in the same study, also reported the majority of CoNS being untypeable by using the published ccr and mec PCR methods. The identification of the prototypic SCCmec type III from eight isolates as well as a type III variant from another eight isolates from different staphylococcal species and different animals suggests horizontal transfer of SCCmec in CoNS from animal origin. As SCCmec type III is one of the SCCmec types that are associated with hospital-acquired MRSA (Deurenberg et al. 2005), it is reasonable to assume that CoNS of animal origin share a common pool of SCCmec with MRSA and thus put a potential threat to public health. The identification of two mecA-negative CoNS with SCC type III agrees with previous findings by Hansen et al. (2004) that the ccrAB gene pairs and the mec regulatory genes are independent of mecA presence. The results also suggest the potential of SCC in transferring antimicrobial resistance other than methicillin resistance due to the invertase-resolvase activity of the ccr genes. The detection of the mec regulatory genes in five mecA-negative CoNS in this study is interesting as one would assume that the mec regulatory genes always coexist with mecA. Indeed, researchers have reported mecA-positive CoNS with no mec regulatory genes (Ibrahem et al. 2009) as well as mecA-negative Staphylococci carrying part of mecI (Shore et al. 2008). This, together with our findings, suggests that the mecA complex may undergo significant genetic exchange during its evolution and partial deletion in the mec regulatory genes may occur before mecA transfers.
Another significance of this study is the recovery of SCCmec type IV in the single S. epidermidis from chicken. S. epidermidis carrying SCCmec type IV has been suggested to be responsible for the conversion of commensal S. aureus to MRSA (Hiramatsu et al. 2001). The relatively smaller size of SCCmec type IV compared to other SCCmec types (Oliveira and de Lencastre 2002) determines the ease of its transfer among staphylococci, which is partially evidenced by the findings of different genomic backgrounds from which SCCmec type IV was detected (Fey et al. 2003). The mecI-negative S. epidermidis isolate with deletion in mecR1 in our study is in line with the previously published hypothesis that deletion in the mec regulatory genes occurred before mecA was transferred from CoNS to methicillin-susceptible S. aureus (Hanssen et al. 2004). Further study on S. epidermidis with SCCmec type IV in animals as well as comparison of CoNS of animal and human origin in regards to their SCC compositions at the molecular level will improve our knowledge on CoNS of animal origin as a potential reservoir of methicillin resistance.

The heterogeneity of SCCmec types in CoNS is also reflected by the different combinations of the mec regulatory genes and Tn554 demonstrated in isolates carrying the same SCCmec types. The presence of non-designated SCCmec types in most isolates indicates novel and largely uncharacterized SCCmec types in CoNS. The detection of mecA without ccrAB genes implies that there may be genetic variants of ccr genes that were not detected by PCR in the current study or unknown mechanisms and/or vectors other than SCC might involve in methicillin resistance transfer among staphylococci.

The data support clonal distribution of CoNS in the animal production environment as evidenced by the findings of identical clones in different farms of the same animal species. Isolates 40 and 51, both S. lentus with identical PFGE patterns, were recovered from different sheep farms on two different dates, suggesting that certain CoNS strains may have a widespread distribution in animals and adapt well in the environment. The fact that same SCCmec type existed in different species of CoNS and topoisomerase genes in fluoroquinolone- and methicillin-resistant Staphylococcus pseudintermedius imply that there may be genetic variants of ccr genes that were not detected by PCR in the current study or unknown mechanisms and/or vectors other than SCC might involve in methicillin-resistance transfer among staphylococci.

This is evidenced by the fact that most isolates of different species with identical PFGE patterns also demonstrated different SCC typing results, except for those isolates with no ccr or mec regulatory genes detected.

In conclusion, diverse SCCmec types are present in CoNS of animal origin. Methicillin-resistant CoNS of animal origin and MRSA may share a common pool of mec complex. Both clonal distribution of methicillin-resistant CoNS and horizontal transfer of SCC with mecA among CoNS occur in animals. Future research effort on molecular epidemiology of methicillin-resistant CoNS and possible transmission of mecA between CoNS and S. aureus from both animal and human sources needs to be addressed to gain more insights into the emergence and transfer mechanisms of methicillin resistance in staphylococci.

References


