

REVIEW ARTICLE

Nasal *Staphylococcus aureus* and *S. pseudintermedius* carriage in healthy dogs and cats: a systematic review of their antibiotic resistance, virulence and genetic lineages of zoonotic relevance

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Abstract

The molecular ecology of *Staphylococcus aureus*, *Staphylococcus pseudintermedius* and their methicillin-resistant strains in healthy dogs and cats could serve as good models to understand the concept of bacterial zoonosis due to animal companionship. This study aims to provide insights into pooled prevalence, genetic lineages, virulence and antimicrobial resistance (AMR) among healthy dogs and cats. Original research and brief communication articles published from 2001 to 2021 that reported the nasal detection of *S. aureus* and *S. pseudintermedius* in healthy dogs and cats in the community, homes and outside veterinary clinics were examined and analysed. Forty-nine studies were eligible and included in this systematic review. The pooled prevalence of nasal carriage of *S. aureus*/methicillin-resistant *S. aureus* (MRSA) in healthy dogs and cats were 10.9% (95% CI: 10.1–11.9)/2.8% (95% CI: 2.4–3.2) and 3.2% (95% CI: 1.9–4.8)/0.5% (95% CI: 0.0–1.1), respectively. Conversely, the pooled prevalence of *S. pseudintermedius*/methicillin-resistant *S. pseudintermedius* (MRSP) in healthy dogs and cats were 18.3% (95% CI: 17.1–19.7)/3.1% (95% CI: 2.5–3.7) and 1.3% (95% CI: 0.6–2.4)/1.2% (95% CI: 0.6–2.3), respectively. Although highly diverse genetic lineages of *S. aureus* were detected in healthy dogs and cats, MSSA-CC1/CC5/CC22/CC45/CC121/CC398 and MRSA-CC5/CC93/CC22/CC30 were mostly reported in dogs; and MSSA-CC5/CC8/CC15/CC48 and MRSA-CC22/CC30/CC80 in cats. Of note, MSSA-CC398 isolates (*spa*-types t034 and t5883) were detected in dogs. Genetic lineages often associated with MSSP/MRSP were ST20/ST71, highlighting the frequent detection of the epidemic European MRSP-ST71 clone in dogs. *S. aureus* isolates carrying the *luk-S/F-PV*, *tst*, *eta*, *etb* and *etd* genes were seldomly detected in dogs, and *luk-S/F-PV* was the unique virulence factor reported in isolates of cats. *S. pseudintermedius* isolates harbouring the *luk-S/F-I*, *seint* and *expA* genes were frequently found, especially in dogs. High and diverse rates of AMR were noted, especially among MRSA/MRSP isolates. There is a need for additional studies on

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the molecular characterization of isolates from countries with under-studied nasal staphylococci isolates.

KEYWORDS

healthy cats, healthy dogs, MRSA, MRSP, MRSP-ST71, MSSA-CC398, nasal carriage, *Staphylococcus aureus*, *Staphylococcus pseudintermedius*, zoonosis

INTRODUCTION

Staphylococcus aureus (*S. aureus*) and *Staphylococcus pseudintermedius* (*S. pseudintermedius*) are considered part of the nasal microbiota of healthy humans and dogs/cats, respectively, but can also become opportunistic pathogens (Abdullahi, Lozano, et al., 2021; Ruiz-Ripa et al., 2021). In the nasal cavities of these pets, *S. pseudintermedius* is more frequently detected than *S. aureus* (Bannoehr & Guardabassi, 2012; Ruiz-Ripa et al., 2021). *S. pseudintermedius* is a significant aetiological agent of pyoderma, soft tissue, urinary tract and ear infections in dogs (Bannoehr & Guardabassi, 2012; Lynch & Helbig, 2021). Although humans are not the natural host of *S. pseudintermedius*, this microorganism could cause infections in persons with close contact with infected/colonized dogs (zoonotic transmission) (Carroll et al., 2021; Lozano et al., 2017).

S. pseudintermedius, described in Devriese et al. (2005), belongs to the *Staphylococcus intermedius* group (SIG) which encompasses four additional species, viz; *S. intermedius*, *S. delphini*, *S. cornubiensis* and *S. ursi* (Carroll et al., 2021). The last two species have been very recently described (Murray et al., 2018; Perreten et al., 2020). *S. pseudintermedius* is the most common skin commensal in dogs (Bannoehr & Guardabassi, 2012; Ma, Worthing, Ward, et al., 2020), but it is less prevalent in cats due to differences in skin cell adherence factors (Bierowiec et al., 2021; Mališová et al., 2019). This species can also be isolated in healthy donkeys or wild boar, among others (Gharsa, Slama, et al., 2015; Mama et al., 2019). In the earlier 2000s, *S. pseudintermedius* could not be accurately distinguished from *S. intermedius* using biochemical methods. Therefore, it was often incorrectly identified as *S. intermedius* (Börjesson et al., 2015).

Methicillin-resistant *S. aureus* (MRSA) represents a major challenge in human and animal infection control. Methicillin-resistant *S. pseudintermedius* (MRSP) has also become a global health problem in veterinary medicine and both *S. aureus*/MRSA and *S. pseudintermedius*/MRSP are of zoonotic relevance. The *mecA* or *mecC* genes are responsible for methicillin resistance and confer reduced affinity for beta-lactam antimicrobials, and *mecA* is found in most MRSA/MRSP isolates.

Staphylococcus aureus/MRSA nasal carriage in dogs and cats could be an indicator of increased risk of colonization/infection for persons in-contact with these animals by virtue of transmission processes in their shared household (Gómez-Sanz, Torres, Lozano, et al., 2013). Available molecular typing data revealed that companion animals could be carriers of *S. aureus*/MRSA human-associated clonal lineages of livestock-associated (LA) MRSA clones, which suggests reverse zoonosis and jump among hosts (Gómez-Sanz, Torres, Lozano, et al., 2013). In addition to MRSA, available literature has also highlighted MRSP as one of the most concerning multidrug-resistant staphylococci in pets' health. There have been increasing reports of MRSP colonization and infection with high multidrug resistance in dogs and cats (Bierowiec et al., 2021; Lord et al., 2022; Papić et al., 2021).

It is crucial to have close surveillance on MRSP and MRSA in companion animals in place to determine their burden and direct adequate infection control in veterinary hospitals and the human-pet interface. While the molecular epidemiology of clinical MRSA and MRSP isolates in small animals has often been explored, very few have assessed the nasal carriage of *S. aureus* and *S. pseudintermedius* in healthy dogs and cats. Regarding *S. pseudintermedius*, molecular analysis has revealed that the global MRSP population are very diverse and have been identified in pets (Pires Dos Santos et al., 2016). Using MultiLocus Sequence Typing (MLST), studies have demonstrated between-country variations in common sequence types (STs) (Perreten et al., 2010; Pires Dos Santos et al., 2016). For *S. aureus* in pets, the mainly reported genetic lineages of MRSA in dogs and cats often depend on the geographical location, health status of pets and occupation of pets' owners. For instance, community-associated MRSA (eg. CC22, CC30, CC5) and LA-MRSA (e.g. CC398) clones have been widely reported (Aires-de-Sousa, 2017; Chuehahan et al., 2021; Gómez-Sanz, Torres, Lozano, et al., 2013; Ma, Worthing, Gottlieb, et al., 2020; Quitoco et al., 2013).

A recent global health research strategy emphasized the imperative need for an integrated surveillance system in the 'One Health' context of antimicrobial resistance (AMR) profiles of zoonotic bacteria including *Staphylococcus* spp (Dafale et al., 2020). Given the significant role of animals in the transmission of *Staphylococcus*

sp. across other ecosystems (human and environment), the present study was designed to investigate the pattern and pooled prevalence of *S. aureus*, MRSA, *S. pseudintermedius* and MRSP in healthy dogs and cats and to provide a comprehensive review, analysing extracted data on their AMR, virulence and genetic lineages in the past two decades over the world.

METHODOLOGY

Study design

This systematic review was developed and executed on cross-sectional studies that reported *S. aureus*, *S. pseudintermedius*, MRSA and/or MRSP in the nasal cavities of healthy dogs and cats. This study did not require formal ethical approval, as the data used were obtained from previously published findings. This systematic review was based on the guidelines of Preferred Reporting Items for Systematic reviews and Meta-analyses (PRISMA) (<http://prisma-statement.org/PRISMAstatement/checklist.aspx>, accessed on 1 October 2021). All literature describing canine and feline isolates formerly identified as *S. intermedius* will be referred to as *S. pseudintermedius*, unless otherwise shown by genomic investigation. Special focus was given to MRSA, MRSA-CC398, MRSA-CC22, MRSA-CC1, MRSA-CC5 and MSSA-CC398 among dogs/cats. Also, data about the AMR phenotypes and virulence genes were extracted.

Articles search strategy

This was a systematic and synthesizing review on nasal carriage of healthy dogs and cats by *S. aureus*, *S. pseudintermedius*, MRSA and/or MRSP. The entire literature search strategy, the selection of suitable published articles, the data extraction, the presentation of results and the statistical analyses were performed following the PRISMA guidelines. Published articles covering any or a combination of *S. aureus*, *S. pseudintermedius* and their methicillin-susceptible/resistant strains were reviewed using PubMed/Medline, Scopus, Google scholar, Ajol, Embase, ScieLo and Web of Science databases. Original researches and brief communications (reports) published (in English) from 1 January 2001 to 1 October 2021 were searched in these databases. Studies were searched and identified using the medical subject headings (MeSH) or article titles or abstracts. For that, the following MeSH key words combination were used: “nasal *S. aureus* carriage in dogs”, “nasal *S. aureus* carriage in cats”, “Methicillin-Resistant *Staphylococcus aureus* in dogs”,

“Methicillin-Resistant *Staphylococcus aureus* in cats”, “nasal MRSA in healthy dogs”, “nasal MSSA in healthy dogs”, “nasal MRSA in healthy cats”, “nasal MSSA in healthy cats”, “Methicillin-Resistant *Staphylococcus pseudintermedius* in healthy cats”, “Methicillin-Resistant *Staphylococcus pseudintermedius* in healthy dogs”, “nasal MRSP in healthy dogs”, “nasal MRSP in healthy cats”, “nasal *Staphylococcus pseudintermedius* in healthy dogs” and “nasal *Staphylococcus pseudintermedius* in healthy cats”. All eligible studies were scrutinized to identify potential articles from their reference lists. This study did not limit the search by any geographical location.

Inclusion criteria

Articles with appropriate and sufficient data about the prevalence of ‘*S. aureus*, *S. pseudintermedius*, MRSA and/or MRSP nasal carriage’, in healthy dogs/cats (pets in the community, outside veterinary clinics) were selected and extensively reviewed. Data from these studies were extracted and utilized to determine the pooled prevalences of *S. aureus*, *S. pseudintermedius*, MRSA and MRSP nasal carriages in healthy dogs and cats (studies with sample size higher than 10). To avoid error from data selections, the pooled prevalence values were computed from only studies with a cross-sectional design. A dog or cat was considered healthy if there was no reported history of current disease or illness and no abnormalities detected on full physical examination in the eligible study. The MRSA or MRSP status was defined by the identification of resistance by phenotypic methods (using oxacillin or ceftiofur, according to the susceptibility method used and the microorganism) and/or *mecA* positivity by polymerase chain reaction (PCR) or agglutination tests.

All original or brief communication studies on the molecular typing of *S. aureus*, *S. pseudintermedius*, MRSA and/or MRSP in healthy dogs and cats regardless of whether they were cross-sectional or not were considered and included in the systematic review of genetic lineages of data of the isolates. Also, this was regardless of the number of animals tested in contrast to the criterion for determination of pooled prevalence (i.e. a sample size of >10). The search also included *S. intermedius* as well for the dates prior to the accurate discrimination of *S. intermedius* and *S. pseudintermedius*.

Exclusion criteria

(i) Studies that contained duplicate data or were overlapping articles; (ii) reviews and conference abstracts; (iii) cross-sectional studies that included fewer than 10 dogs

or cats; (iv) studies on sick or healthy dogs and cats in the veterinary clinics and hospitals, (v) studies on dogs or cats owned by a veterinarian, (iv) studies on wound scrapings, buccal, tracheal, skin, ear, faecal and other animal samples were excluded.

Data extraction process

Where possible and appropriate, authors; year of study; study design; study setting or location; the number of *S. aureus*, *S. pseudintermedius*, MRSP, MRSA, MSSP, and/or MSSA isolates; type of specimen; laboratory method employed for detection; antimicrobial susceptibility phenotypes and corresponding genotypes and molecular types were reviewed and extracted. When there was disagreement, the relevant paper was reviewed, and the differences were resolved by the authors' consensus. Finally, 49 full-text articles were included. These directly focused on the distribution pattern of the *S. aureus*, MRSA, *S. pseudintermedius*, MRSP, genetic lineages, AMR phenotypes and genotypes, and/or virulence genes in nasal cavities of healthy dogs and cats.

Statistical analysis

The pooled prevalence of nasal carriage of *S. aureus*, MRSA, *S. pseudintermedius* and MRSP was calculated. MedCalc version 20.013 was used for all statistical analyses. Where possible, analyses of pooled prevalence and corresponding 95% confidence intervals (CI) were carried out using the random-effects model. The pooled prevalence was computed by combining the results of the numbers of positive cases and the total number of animals (studied) obtained from eligible multiple cross-sectional studies. Essentially, it involved dividing net sum positives (for *S. aureus*, *S. pseudintermedius*, MRSA, MRSP) by the entire population of healthy dogs or cats (included in each study).

MAIN FINDINGS AND DISCUSSION

Studies characteristics

Out of the 49 eligible and analysed studies (Figure 1), 47 and 13 were on *S. aureus* and/or *S. pseudintermedius*/*S. intermedius* nasal carriage in healthy dogs and cats, respectively (Table S1). Of these, three studies on healthy dogs or cats reported *S. intermedius* instead of *S. pseudintermedius* (Chasioti et al., 2019; Elnageh et al., 2021; Epstein et al., 2009); however, due to suspected

misidentification, all the *S. intermedius* isolates for dogs/cats were considered as *S. pseudintermedius* for this systematic review. It is important to remark that some studies simultaneously investigated staphylococci in both dogs and cats. Table S1 shows the characteristics and data of the eligible studies, countries of the studies, type of pets (divided into dogs and cats), number of pets tested, number of *S. aureus*, *S. pseudintermedius* and MRSA/MRSP obtained from the studies, and the AMR phenotypes and genes, as well as the virulence factors detected from *S. aureus* and/or *S. pseudintermedius* isolates.

The pooled prevalence of nasal carriage of *S. aureus*, *S. pseudintermedius*, MRSA and MRSP in healthy dogs and cats

The pooled prevalence of nasal carriage of *S. aureus* in healthy dogs and cats was 10.9% (95% CI: 10.1–11.9) and 3.2% (95% CI: 1.9–4.8) respectively (Table 1). Although, relatively low when compared to the pooled prevalence of nasal *S. aureus* carriage in healthy humans (15.9%) and nasotracheal carriage in healthy wild animals (18.5%) (Abdullahi, Fernández-Fernández, et al., 2021; Abdullahi, Lozano, et al., 2021), the pooled prevalence of nasal *S. aureus* carriage in healthy dogs was higher than in cats. The reason for this observation is not fully understood as both dogs and cats frequently come in close contact with humans in the household environment, showing a similar risk of *S. aureus* acquisition from humans.

From our analysis, the pooled prevalence of nasal carriage of *S. pseudintermedius* in dogs and cats was 18.3% (95% CI: 17.1–19.7) and 1.3% (95% CI: 0.6–2.4), respectively (Table 1). *S. pseudintermedius* carriage is frequently higher in healthy dogs than in healthy cats. Moreover, comparing *S. pseudintermedius* and *S. aureus* carriage, *S. pseudintermedius* carriage is also higher than *S. aureus* in these animals. *S. pseudintermedius* is considered an opportunistic pathogen that could cause severe and necrotizing infections of the skin, ears, bones and post-surgical abscesses (Bannoehr & Guardabassi, 2012). Moreover, *S. pseudintermedius* could also be found in humans acquired by zoonotic transmission from colonized dogs (Carroll et al., 2021; Lozano et al., 2017; Somayaji et al., 2016) and may be misdiagnosed as *S. aureus* in human infections (Börjesson et al., 2015). To the best of our knowledge, no study determined the pooled prevalence of *S. pseudintermedius* nasal carriage in healthy dogs. Differences were observed in the prevalence of *S. pseudintermedius* nasal carriage among the eligible studies; for instance, some reported a very high prevalence (74.7%) (Garbacz et al., 2013). This difference in prevalence is multifactorial,

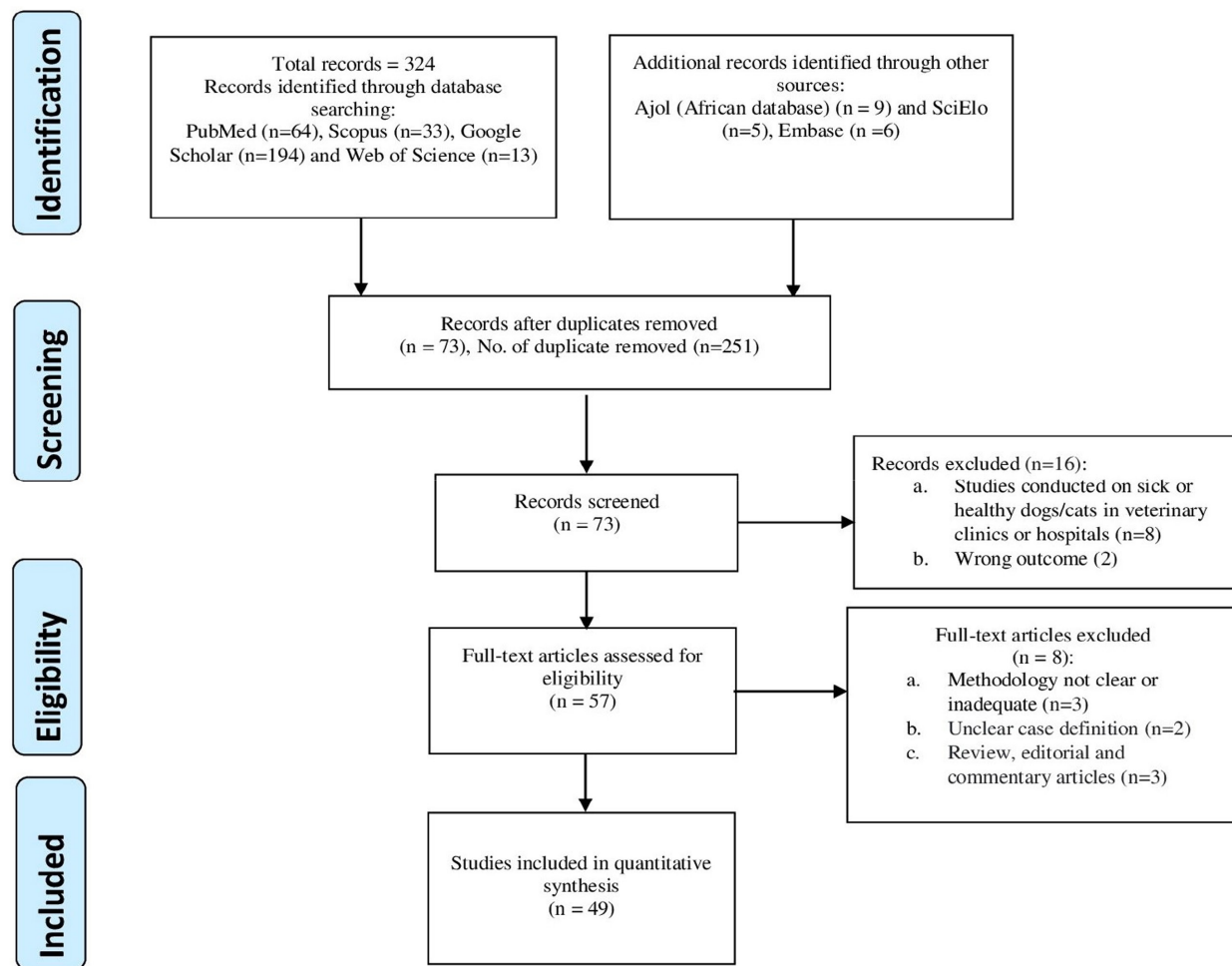


FIGURE 1 Identification and selection flowchart of articles on the nasal *S. aureus* and *S. pseudintermedius* carriage in healthy dogs and cats.

it could be related to the environment of the dogs, and owners' and animals' health statuses.

In relation to MRSA, the growing concern about the spread of MRSA in communities has led to the establishment of recommendations for surveillance, including research into the rate of colonization in healthy dogs, including stray dogs present in public areas. The pooled prevalence of canine MRSA nasal carriage (2.8% [95% CI: 2.4–3.2]) was relatively higher than that of the feline carriage (0.5% [95% CI: 0.0–1.1]) (Table 1). The exposure of pets to their living environment or persistently colonized humans or other animals can be considered a risk factor for colonization with MRSA strains; thus, it is essential to identify community and environmental reservoirs and sources of MRSA in healthy dogs and cats (Mohamed et al., 2020). MRSA nasal carriage in healthy cats was detected by five studies in Libya, the United States, Brazil, the United Kingdom and Saudi Arabia (Elmoslemany et al., 2021; Elnageh et al., 2021; Gingrich et al., 2011; Loeffler et al., 2011; Quitoco et al., 2013) (Table S1). Moreover, nasal MRSA in healthy dogs has been studied

and detected in all continents (Table S1). From our analysis, the pooled prevalence of nasal carriage of MRSP in dogs and cats was 3.1% (95% CI: 2.5–3.7) and 1.2% (95% CI: 0.6–2.3) respectively (Table 1).

The complex relationships between bacterial species from different hosts facilitate genetic flow, extending AMR between humans, animals and the environment, resulting in public health concerns. Of this, methicillin resistance is one of the major and significant AMR of zoonotic importance. A companion animal may play an important role in the maintenance and transmission of MRSP or MRSA in the household (Gómez-Sanz, Torres, Lozano, et al., 2013).

It is important to remark that there was a variation in the pooled prevalence of *S. aureus*/*S. pseudintermedius* and MRSA/MRSP across the continents (Figure 2). Nevertheless, when interpreting these data, it should be noted that they may be influenced by regional or local epidemiologies of *S. aureus*/*S. pseudintermedius*. Particularly, the pooled MRSA and MRSP prevalence were highest in Africa and Asia respectively. In these cases, these variations could also be due to differences in used methodologies,

TABLE 1 Summary of the pooled global prevalence of *Staphylococcus aureus*, *S. pseudintermedius*, MRSA and MRSP nasal carriage in healthy dogs and cats

Animals	Number of <i>S. aureus</i> publications included		Total number of		Pooled prevalence of <i>S. aureus</i> nasal carriage		Number of MRSA publications included		Total number of		Pooled prevalence of MRSA nasal carriage	
	Animals	<i>S. aureus</i>	Animals	<i>S. aureus</i>	% (95% CI)	% (95% CI)	Animals	MRSA	Animals	MRSA	% (95% CI)	% (95% CI)
Dogs	34	544	4946	544	10.9 (10.1–11.9)	38	5815	161	5815	2.8 (2.4–3.2)	47	
Cats	10	21	666	21	3.2 (1.9–4.8)	11	1052	5	1052	0.5 (0.0–1.1)	13	

Animals	Number of <i>S. pseudintermedius</i> publications included		Total number of		Pooled prevalence of <i>S. pseudintermedius</i> nasal carriage		Number of MRSP publications included		Total number of		Pooled prevalence of MRSP nasal carriage	
	Animals	<i>S. pseudintermedius</i>	Animals	<i>S. pseudintermedius</i>	% (95% CI)	% (95% CI)	Animals	MRSP	Animals	MRSP	% (95% CI)	% (95% CI)
Dogs	26	633	3453	633	18.3 (17.1–19.7)	28	3716	114	3716	3.1 (2.5–3.7)	47	
Cats	8	10	757	10	1.3 (0.6–2.4)	8	744	9	744	1.2 (0.6–2.3)	13	

Abbreviations: MRSA, methicillin-resistant *S. aureus*; MRSP, methicillin-resistant *S. pseudintermedius*.

and other potential reasons such as pets care (especially animal hygiene), environmental sanitation or antibiotic use in animals and humans in these continents (Collignon & Voss, 2015; Fletcher, 2015; Valiakos et al., 2020).

Antibiotic resistance phenotypes and genotypes of *S. aureus* and *S. pseudintermedius* detected from nasal cavities of healthy dogs and cats

In the studies included in this systematic review, it appeared that both MRSA and MSSA had resistance against non-beta-lactam antimicrobials, such as fluoroquinolones, aminoglycosides, tetracyclines, sulphonamides, macrolides, and/or lincosamides (Tables 2 and 3). Based on the WHO classification of antimicrobials into highly important versus critically important classes of antimicrobial agents (World Health Organization, 2017), some antibiotics of zoonotic relevance in each class are discussed below.

Regarding methicillin resistance, out of the 21 studies that reported nasal MRSA in healthy dogs or cats, 17 investigated and detected the *mecA* gene. However, none reported the *mecC* gene (Tables 2 and 3). In dogs, *S. aureus* isolates were frequently resistant to tetracycline, aminoglycosides, rifampicin, sulphonamides and/or chloramphenicol (Table 2). *S. pseudintermedius* strains presented wider AMR patterns (phenotype and genotype) than those reported in nasal *S. aureus* of healthy dogs. In a recent study, *S. pseudintermedius* from dogs showed more frequently a MDR phenotype (45.5%) than *S. aureus* (40.9%) in a collection of isolates obtained between 2007 and 2016 (Lord et al., 2022).

Aside from the cefoxitin/oxacillin resistance detected in MRSA and MRSP, sulfamethoxazole-trimethoprim and ciprofloxacin resistances were the most predominant in healthy cats (reported in 4 and 3 out of 5 studies respectively). Other antibiotic resistances detected included erythromycin and clindamycin (inducible), amikacin, enrofloxacin and tetracycline (Table 3). Remarkably, Gómez-Sanz, Torres, Lozano, et al. (2013) detected the resistance genes *tet(M)*, *erm(B)*, *aphA*, *aadE* and *sat4* in MSSP isolates from healthy cats in Spain. Moreover, Rynhoud et al. (2021) detected some genes responsible for sulfamethoxazole-trimethoprim and aminoglycoside resistance in MRSP (*dfgG* and *aac(6')-aph(2'')*), *aadD*, *ant6-Ia*, and/or *aph3-III* respectively). A wide variation in *S. aureus* resistance patterns was detected in many studies, but penicillin and ciprofloxacin resistances were frequently detected in *S. aureus* and *S. pseudintermedius* that colonize healthy cats (Table 3). MDR phenotype has also been reported to be common among *S. pseudintermedius* strains from diseased pets (100.0%) than healthy ones (73.0%) (Rynhoud et al., 2021).

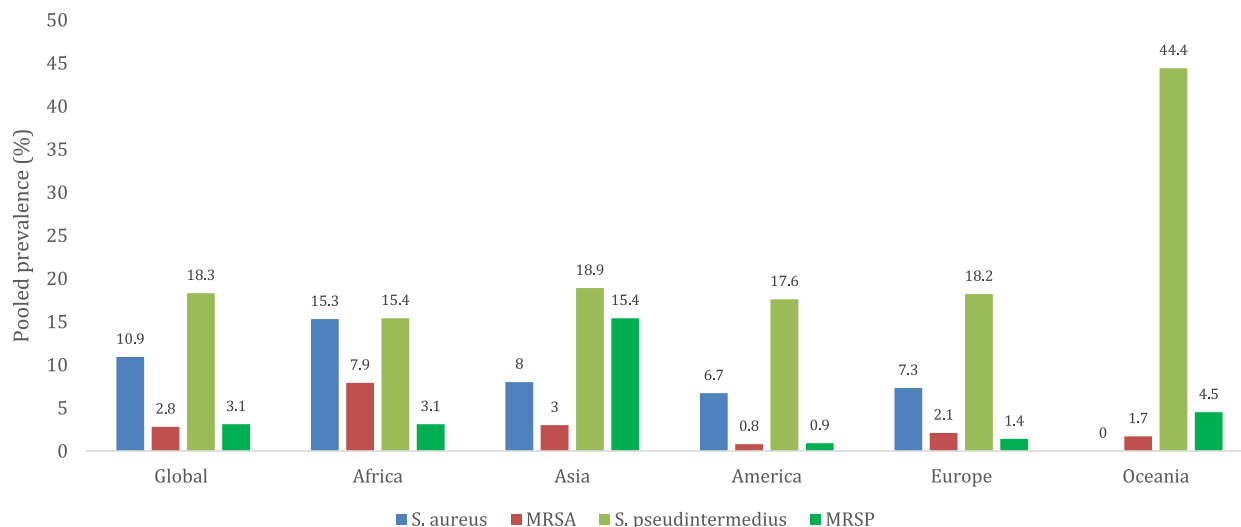


FIGURE 2 Pooled prevalence of *Staphylococcus aureus*, MRSA, *S. pseudintermedius* and MRSP nasal carriage among healthy dogs by continents. Note: In each continent, the indicated pooled prevalence was analyzed independently. The number of studies per continent in *S. aureus*, MRSA, *S. pseudintermedius* and MRSP, respectively, were as follows: Africa (9, 8, 6, and 6); Asia (11, 10, 6, 5); America (3, 7, 4, and 5), Europe (9, 10, 8, and 8) and Oceania (0, 1, 1, and 3). MRSA, methicillin-resistant *S. aureus*; MRSP, methicillin-resistant *S. pseudintermedius*.

Focusing on some antimicrobials of great importance for human and animal health (or for epidemiological purposes), tetracycline resistance was reported in healthy cats in only one study related to MSSA isolates in Saudi Arabia (Elmoslemay et al., 2021). In contrast, tetracycline resistance was detected in nasal MRSA and MSSA isolates from healthy dogs in 12 studies (Table 2). Specifically, out of the 61 pooled MRSA isolates from nasal cavities of healthy dogs, 24 (39.3%) were tetracycline resistant. However, eight (8.9%) out of the 89 pooled MSSA isolates from eligible studies were tetracycline resistant (data obtained from Table 2). The lineages MSSA-ST1212/t582, MSSA-ST121/t159 and MRSA-ST59 were detected among tetracycline-resistant isolates (Gharsa, Ben Slama, et al., 2015; Gómez-Sanz, Torres, Lozano, et al., 2013; Wan et al., 2012). The elevated frequency of tetracycline resistance found may be related to the frequent use of this antimicrobial agent (firstline) in dogs and cats. This phenotype of resistance has been proposed as a good marker of MRSA isolates belonging to clonal lineages associated with livestock animals, especially CC398 (Benito et al., 2014; Ceballos et al., 2020). Tetracycline resistance was also very common among *S. pseudintermedius* isolates.

In relation to nasal *S. aureus* strains from healthy dogs, many studies reported the detection of erythromycin resistance (Table 2). Similarly, two studies reported the erythromycin-clindamycin inducible resistance phenotype in nasal *S. pseudintermedius* isolates from healthy dogs and cats (Gómez-Sanz, Torres, Lozano, et al., 2013; Van Balen et al., 2017).

Recently, an increasing penicillin susceptibility rate is being detected among invasive MSSA human isolates, opening therapeutic opportunities for these infections; this phenotype has been frequently found among *scn*-negative or CC398 isolates suggesting a potential animal association (Mama, Aspiroz, Lozano, et al., 2021). In this review, penicillin susceptibility was reported in 79.2% ($n = 19$) of the MSSA isolates detected from healthy dogs by Gómez-Sanz, Torres, Benito, et al. (2013), and seven of these isolates (36.8%) belonged to the CC398 clone.

In healthy dogs, four studies also reported varying ciprofloxacin resistance among nasal *S. aureus* isolates, with a range of 40.7%–100.0% (Abdel-Moein et al., 2012; Coelho et al., 2011; Myaing et al., 2016; Wedley et al., 2014). Of the four studies, the pooled prevalence of ciprofloxacin resistance in *S. aureus* nasal isolates from healthy dogs was 53.9% (55 out of 102 isolates). Ciprofloxacin resistance was reported in *S. aureus* isolates in two studies of healthy cats (Elnageh et al., 2021; Gharsa, Ben Slama, et al., 2015). None of the *S. aureus* studies reported the molecular mechanisms implicated. In the case of *S. pseudintermedius*, the GyrA [Ser84Leu, Glu714Lys, Ser84Leu] and GrlA [Ser80Ile] amino acids substitutions were reported from MRSP isolates of healthy dogs in one unique study (Gómez-Sanz et al., 2011); these mutations are associated with decreased susceptibility to ciprofloxacin and other fluoroquinolones in staphylococci (Rynhoud et al., 2021).

Nine studies of healthy dogs or cats reported gentamicin resistance in *S. aureus* (Table 2), but only one of these studies indicated the bifunctional gene, *aac(6′)-aph(2′)* as the mechanism implicated (Coelho et al., 2011).

TABLE 2 Antimicrobial resistance phenotypes and genotypes of *Staphylococcus pseudintermedius* and *S. aureus* isolates from the nasal cavities of healthy dogs

Reference	Country	Sample size	No. of <i>S. aureus</i> (%) / MRSA (%)	No. of <i>S. pseudintermedius</i> (%) / MRSP (%)	Antimicrobial resistance phenotype	Antimicrobial resistance genes
Katakweba et al. (2016)	Tanzania	100	11 (11.0)/0 (0.0)	ND	SA: AMP, TET	NT
Wachtmeister (2018)	Uganda	39	5 (12.8)/2 (5.1)	10 (25.6)/0 (0.0)	SA: ERY, FOX, TET SP: CLI, ERY, ENR, GEN, PEN, SXT, TET	MRSA: <i>mecA</i>
Mustapha et al. (2016)	Nigeria	211	78 (36.9)/50 (23.7)	ND	SA: CLI, ERY, FOX, OXA, TET	MRSA: <i>mecA</i>
Daodu et al. (2016)	Nigeria	173	31 (14.0)/NT	NT	SA: AMP, GEN, STR, SXT	NT
Moses et al. (2020)	Nigeria	35	ND	25 (71.4)/18 (51.1)	SP: AMP, CHL, CIP, LEV, OFL, OXA	MRSP: <i>mecA</i>
Abdel-Moein et al. (2012)	Egypt	48	1 (2.1)/1 (2.1)	NT	SA: CLI, CIP, FOX, GEN, OXA, RIF, SXT	MRSA: <i>mecA</i>
Gharsa et al. (2013)	Tunisia	100	ND	55 (55.0)/0 (0.0)	SP: CHL, CIP, CLI, ERY, KAN, PEN, SXT, TET	SP: <i>aph(3')-Ia, erm(B), ant(6)-Ia, blaZ, tet(M)</i>
Gharsa, Ben Slama, et al. (2015)	Tunisia	100	4 (4.0)/0 (0.0)	ND	SA: ERY, PEN, TET	SA: <i>bla(Z), tet(M), erm(A), ant(6)-Ia</i>
Quitoco et al. (2013)	Brazil	70	NR/0 (0.0)	NR/1 (1.4)	MRSP: CLI, CHL, FOX, ERY, GEN, OXA, PEN, TET	MRSP: <i>mecA</i>
Fabri et al. (2021)	Brazil	241	38 (15.8)/3 (1.2)	ND	SA: FOX, OXA	MRSA: <i>mecA</i>
Penna et al. (2021)	Brazil	88	NT/3 (3.4)	NT	MRSA: CHL, ENR	MRSA: <i>mecA</i>
Rubin and Chirino-Trejo (2011)	Canada	175	ND	75 (42.9)/0 (0.0)	SP: PEN, ERY, CLI, TET	NT
Van Balen et al. (2017)	USA	113	7 (8)/0 (0.0)	NT	AMP, ERY, CLI- ^{Ind}	ND
Han et al. (2015)	South Korea	92	NT	32 (34.8)/22 (23.9)	MRSP: OXA	MRSP: <i>mecA</i>
Wan et al. (2012)	Taiwan	776	20 (2.6)/1 (0.13)	NT	SA: CHL, CLI, ERY, FOX, GEN, OXA, TET	MRSA: <i>mecA</i>

(Continues)

TABLE 2 (Continued)

Reference	Country	Sample size	No. of <i>S. aureus</i> (%) / MRSA (%)	No. of <i>S. pseudintermedius</i> (%) / MRSP (%)	Antimicrobial resistance phenotype	Antimicrobial resistance genes
Boost et al. (2007)	Hong Kong	815	73 (8.9)/6 (0.74)	NT	SA: CLI, CHL, ERY, GEN, OXA, PEN, SXT, TET	NT
Epstein et al. (2009)	Hong Kong	35	0 (0.0)/0 (0.0)	NR/6 (17.1)	MRSP: FOX, GEN, PEN	NT
Myaing et al. (2016)	Myanmar	65	NR/31 (47.7)	NT	MRSA: AMP, CLI, CIP, ERY, LZD, RIF, SXT, TET	NT
Rahman et al. (2018)	Bangladesh	36	9 (25.0)/4 (11.1)	NT	SA: OXA	MRSA: <i>mecA</i>
Decline et al. (2020)	Indonesia	50	24 (48.0)/14 (28.0)	NT	SA: AMK, CLI, ERY, FOX, OXA, PEN, SXT, TET	NT
Sekhar et al. (2017)	India	40	14 (35.0)/5 (12.5)	NR	SA: PEN, FOX	MRSA: <i>mecA</i> , <i>blaZ</i>
Rynhoud et al. (2021)	Australia	61	0 (0.0)/0 (0.0)	NT/7 (11.5)	MRSP: CLI, CHL, ERY, ENR, GEN, SXT, TET	MRSP: <i>mecA</i> , <i>aac(6')-aph(2'')</i> , <i>aadD</i> , <i>ant6-Ia</i> , <i>aph3-III</i> , <i>sat4A</i> , <i>blaZ</i> , <i>ermB</i> , <i>ermC</i> , <i>cat-pC221</i> , <i>dfcG</i> , <i>tet(M)</i>
Gómez-Sanz et al. (2011)	Spain	196	NR	NR/9 (4.6)	MRSP: CLI, ERY, FOX, CIP, GEN, KAN, OXA, STR, SXT, TET, TOB	MRSP: <i>aphA-3</i> , <i>aadE</i> , <i>blaZ</i> , <i>dfc(G)</i> , <i>erm(B)</i> , <i>GyrA</i> [Ser84Leu, Glu714Lys, Ser84Leu] and <i>GrlA</i> [Ser80Ile], <i>tet(K)</i> , <i>sat4</i>
Gómez-Sanz, Torres, Benito, et al. (2013)	Spain	54	5 (9.2)/0 (0.0)	14 (25.9)/2 (3.7)	SA: ERY, CLI ^{ind} , PEN SP: CIP, FUS, GEN, OXA, PEN, TET, TOB	SA: <i>blaZ</i> , <i>erm(A)</i> SP: <i>mecA</i> , <i>aac(6')-aph(2'')</i> , <i>aphA3-aadE</i> -, <i>blaZ</i> , <i>erm(B)</i> , <i>dfc(G)</i> , <i>sat4</i> , <i>tet(K)</i> , <i>tet(M)</i>

TABLE 2 (Continued)

Reference	Country	Sample size	No. of <i>S. aureus</i> (%) / MRSA (%)	No. of <i>S. pseudintermedius</i> (%) / MRSP (%)	Antimicrobial resistance phenotype	Antimicrobial resistance genes
Gómez-Sanz, Torres, Lozano, et al. (2013)	Spain	98	24/0 (0.0)	22 (22.4)/8 (8.2)	SA: CLI ^{ind} , ERI, PEN, STR, TET SP: CLI ^{ind} , CHL, ERY, KAN, PEN, STR, TET	SA: blaZ, erm(C), erm(A), str, tet(K) SP: aphA3, aadE, blaZ, erm(B), sat4, tet(L), tet(M)
Loeffler et al. (2010)	UK	129	NR/10 (7.8)	ND	MRSA: FOX	MRSA: mecA
Loeffler et al. (2011)	UK	302	NR/2 (0.66)	NT	MRSA: FOX	MRSA: mecA
Schmidt et al. (2014)	UK	73	6 (8.2)/0 (0.0)	32 (43.8)/0 (0.0)	SA: FUS, GEN, TET SP: CIP, FUS, GEN, TET,	NT
Wedley et al. (2014)	UK	724	54 (7.5)/7 (0.9)	80 (11.0)/0 (0.0)	SA: CIP, FOX, GEN, RIF, TET SP: CIP, GEN, SXT, TET	MRSA: mecA, erm(C)
Coelho et al. (2011)	Portugal	54	NR/16 (29.6)	NR	MRSA: CIP, CLI, ERY, GEN, KAN, TOB	MRSA: mecA, aac(6')-aph(2''), ant(4')-Ia, aph(3')-III, ermB, ermC, msrA, tet(M)
Chasioti et al. (2019)	Greece	33	2 (6.1)/0 (0.0)	0 (0.0)/0 (0.0)	SA: ERY, PEN	NT
Loncaric et al. (2019)	Austria	152	NT	NR/2 (1.3)	MRSP: AMK, CLI, CIP, ERY, GEN, OXA, SXT, TET	MRSP: mecA, aac(6')-aph(2''), dfrG, erm(B), aac(6')-Ie, tet(K)
Bean & Wigmore, 2016	Australia	117	7 (5.9)/0 (0.0)	52 (44.4)/1 (0.85)	SA: PEN SP: PEN, TET, OXA	MRSP: mecA

(Continues)

TABLE 2 (Continued)

Reference	Country	Sample size	No. of <i>S. aureus</i> (%) / MRSA (%)		No. of <i>S. pseudintermedius</i> (%) / MRSP (%)		Antimicrobial resistance phenotype	Antimicrobial resistance genes
			NR	MRSA	0	MRSP		
Ma, Worthing, Gottlieb, et al. (2020)	Australia	303	NR/5 (1.7)		0 (0.0)/0 (0.0)		SA: PEN, FOX, SXT	MRSA: <i>mecA</i> , <i>blaZ</i> , <i>dfgG</i>
Garbacz et al. (2013)	Poland	95	10 (10.5)/0 (0.0)		71 (74.7)/0 (0.0)		SA: AMP, ERY, CLI, NEO, SXT, TET SP: AMP, ERY, CLI, NEO, SXT, TET	NT

Abbreviations: CHL, chloramphenicol; CIP, ciprofloxacin; CLI, clindamycin; ENR, enrofloxacin; ERY, erythromycin; FOX, cefoxitin; GEN, gentamicin; ^{ind}, inducible; KAN, kanamycin; LEV, levofloxacin; LZD, linezolid; MRSA, methicillin-resistant *S. aureus*; MRSP, methicillin-resistant *S. pseudintermedius*; ND, not detected; NR, not reported in detail; NT, not tested; OXA, oxacillin; PEN, penicillin; RIF, rifampicin; SA, *S. aureus*; SP, *S. pseudintermedius*; STR, Streptomycin; SXT, Trimethoprim/sulfamethoxazole; TET, Tetracycline.

Regarding *S. pseudintermedius*, nine studies reported the detection of gentamicin resistance in isolates from healthy dogs (Table 2), however, only four showed the molecular mechanism implicated for this resistance. Different aminoglycoside resistance genes have been detected in the eligible studies (*aac(6′)-aph(2′′)*, *aph(3′)-III*, *aadD*, *ant6-Ia*) (Gómez-Sanz, Torres, Benito, et al., 2013; Gómez-Sanz et al., 2011; Loncaric et al., 2019; Rynhoud et al., 2021).

Genetic lineages associated with *S. aureus* isolates from the nasal cavities of healthy dogs and cats

In relation to nasal MSSA isolates from healthy dogs, the lineages CC1, CC5, CC22, CC45, CC121 and CC398 were predominant, although CC15, CC30, CC88, CC97 and CC133 were also reported; these lineages are generally associated with both humans and animals. Moreover, the lineages CC22 and CC30, that were identified among canine MRSA isolates, are known human-associated clones (Table 4). On the other hand, the lineages CC5, CC15, CC45 and CC8 were found in MSSA isolates of healthy cats, and CC22, CC80 and CC30 among feline MRSA isolates (Table 4).

CC398 is a relevant clonal lineage due to its possible relationship with farm animals or veterinary farmers. In recent years, two CC398 clades have been proposed, one animal subclade more associated with MRSA and one human subclade related to MSSA. The CC398 lineage was reported in healthy dogs in only one study performed in Spain (Gómez-Sanz, Torres, Benito, et al., 2013), in which all isolates were MSSA. The MSSA-ST398 lineage represented 29.2% of the total *S. aureus* isolates recovered from the dogs in this study and no data about the possible contact with livestock were available for these animals. These MSSA-ST398 isolates presented the *spa*-types t034, t108 and t5883 (Table 4). Despite the methicillin susceptibility of these strains (that could suggest the human-related livestock-independent subclade), the detection of the *spa*-type t034 and the absence of the IEC system (*scn*-marker) infer an animal (or livestock) origin (Mama, Aspiroz, Ruiz-Ripa, et al., 2021). MSSA-CC398 isolates have also been detected in wild birds (such as storks), also in Spain, but the isolates presented the *spa*-types t571 and t6606; and were *scn*-positive (Gómez et al., 2016).

Regarding CC133, it is a well-known small ruminant-associated lineage (Guinane et al., 2010), that has been detected as a predominant *S. aureus* lineage in cats in Japan (Sasaki et al., 2012), and in a collection of large felines from a Danish Zoo (Espinosa-Gongora et al., 2012).

Among other STs isolated from dogs, ST1/CC1 was the most frequently reported in most eligible dogs' studies. It is a

TABLE 3 Antimicrobial resistance phenotypes and genotypes of *Staphylococcus pseudintermedius* and *S. aureus* isolates from the nasal cavities of healthy cats

Reference	Country	Sample size	No. of <i>S. aureus</i> (%) / MRSA (%)	No. of <i>S. pseudintermedius</i> (%) / MRSP (%)	Antimicrobial resistance phenotype	Antimicrobial resistance genes
Elnageh et al. (2021)	Libya	62	3 (4.8) / 1 (1.6)	NT	SA: CLI, CIP, ERY, GEN, PEN	MRSA: <i>mecA</i> <i>blaZ</i>
Gharsa, Ben Slama, et al. (2015)	Tunisia	34	2 (5.9) / 0 (0.0)	ND	SA: CIP, PEN	MRSA: <i>mecA</i>
Quitoco et al. (2013)	Brazil	60	NR / 1 (1.7)	NR / 0 (0.0)	MRSA: FOX, OXA	MRSA: <i>mecA</i>
Gingrich et al. (2011)	USA	200	NR / 1 (0.5)	NR / 0 (0.0)	NT	NT
Elmoslemany et al. (2021)	Saudi Arabia	209	5 (2.4) / 1 (0.48)	1 (0.48) / 0 (0.0)	SA: ERY, FOX, GEN, PEN, TET SP: AMK, GEN, PEN, SXT, TET	MRSA: <i>mecA</i>
Gómez-Sanz, Torres, Benito, et al. (2013)	Spain	12	3 (25.0) / 0 (0.0)	1 (8.3) / 0 (0.0)	SA: PEN SP: CLI ^{ind} , CHL, ERY, PEN, STR, TET	SA: <i>blaZ</i> SP: <i>aphA3</i> , <i>aadE</i> , <i>blaZ</i> , <i>catpC221</i> , <i>erm(B)</i> , <i>tet(M)</i> , <i>sat4</i>
Loeffler et al. (2011)	UK	216	NT / 1 (0.46)	NT	MRSA: FOX SP: PEN	MRSA: <i>mecA</i> NT
Chasioti et al. (2019)	Greece	22	0 (0.0) / 0 (0.0)	3 (13.6) / 0 (0.0)	MRSP: CLI, CHL, ENR, ERY, GEN, SXT, TET	MRSP: <i>mecA</i> , <i>aac(6')-aph(2'')</i> , <i>aadD</i> , <i>ant6-Ia</i> , <i>aph3-III</i> , <i>blaZ</i> , <i>cat-pC221</i> , <i>dfrG</i> , <i>ermB</i> , <i>ermC</i> , <i>sat4A</i> , <i>tet(M)</i>
Rynhoud et al. (2021)	Australia	127	0 (0.0) / 0 (0.0)	NT / 9 (7.1)	MRSP: CLI, CHL, ENR, ERY, GEN, SXT, TET	MRSP: <i>mecA</i> , <i>aac(6')-aph(2'')</i> , <i>aadD</i> , <i>ant6-Ia</i> , <i>aph3-III</i> , <i>blaZ</i> , <i>cat-pC221</i> , <i>dfrG</i> , <i>ermB</i> , <i>ermC</i> , <i>sat4A</i> , <i>tet(M)</i>
Ma, Worthing, Gottlieb, et al. (2020)	Australia	80	0 (0.0) / 0 (0.0)	0 (0.0) / 0 (0.0)	NT	NT

Abbreviations: NT, not tested; ND, not detected; NR, not reported in detail; SA, *S. aureus*; SP, *S. pseudintermedius*; MRSA, methicillin-resistant *S. aureus*; MRSP, methicillin-resistant *S. pseudintermedius*; ^{ind}, inducible; AMK, amikacin; CHL, chloramphenicol; CLI, clindamycin; CIP, ciprofloxacin; ENR, enrofloxacin; ERY, erythromycin; FOX, cefoxitin; GEN, gentamicin; PEN, penicillin; RIF, rifampicin; SXT, trimethoprim/sulfamethoxazole; TET, tetracycline.

TABLE 4 Molecular typing reports of *Staphylococcus aureus* isolated from the nasal cavities of healthy dogs and cats

Reference	Country	No. of <i>S. aureus</i> /no. of MRSA	Molecular typing of MSSA (no. of isolates, when available)			Molecular typing of MRSA isolates (no. of isolates, when available)		
			<i>Spa</i> type	ST	CC	<i>spa</i> type	ST	CC
<i>Healthy dog population</i>								
Gharsa, Ben Slama, et al. (2015)	Tunisia	4/0	t701 (2), t582, t178/t701 (2)	ST2121, ST6 (2), ST188, ST6 (2)	CC5 (2), CC15, CC30, CC5 (2)	ND	ND	ND
Katakweba et al. (2016)	Tanzania	11/0	t314/t084, t223, t267, t1476, t508/t127 (4)	ST1 (4), ST121, ST15, ST18, ST22, ST97, ST1 (4)	NR	ND	ND	ND
Van Balen et al. (2017)	USA	7/0	NT	USA600 (3), USA300 (2), USA100 (1), group C (1)	NT	NT	NT	NT
Coelho et al. (2011)	Portugal	NR/16	NR	NR	NR	t032 (7), t747 (6), t432 (2), t4726 (1).	ST22 (4)	NR
Loeffler et al. (2011)	UK	0/2	NT	NT	NT	NT	ST36 (2)	CC30 (2)
Wedley et al. (2014)	UK	758/7	t2133, t304, t026, t660, t012, t019, t1010, t474, t127, t272, t287, t160, t002, t1509, t688	NT	NT	t032 (5), t022 (1), t3213 (1)	NT	NT
Gómez-Sanz, Torres, Benito, et al. (2013)	Spain	24/0	t034 (4), t5883 (2), t108 (1), t186, t002, t177, t8765, t040, t015, t8764	ST398 (7), ST133, ST2329, ST1, ST5, ST146, ST188, ST1655, ST15, ST78, ST45, ST217	CC398 (7), CC133, CC5, CC88, CC45, CC22	NT	NT	NT
Gómez-Sanz, Torres, Lozano, et al. (2013)	Spain	5/0	t021, t073, t159, t151 (2)	ST45, ST121 (3)	CC45, CC121 (3)	ND	ND	ND
Ma, Worthing, Gottlieb, et al. (2020)	Australia	NR/5	NT	NT	NT	t127 (1), t202 (2), other two are non-typeable	ST1 (1), ST5 (1), ST93 (3)	NT
<i>Healthy cat population</i>								
Gharsa, Ben Slama, et al. (2015)	Tunisia	2/0	t279, t701	ST15, ST6	CC5, CC15	ND	ND	ND
Quitoco et al. (2013)	Brazil	NR/1	NT	NT	NT	NT	ST30	NT
Elmoslemany et al. (2021)	Saudi Arabia	5/1	NT	NT	NT	NR	ST80	NR
Rynhoud et al. (2021)	Australia	NT/9	NT	NT	NT	NT	ST496, ST749, ST71, ST316, ST84	NT
Loeffler et al. (2011)	UK	0/2	NT	NT	NT	NT	NR	CC22 (1)
Gómez-Sanz, Torres, Lozano, et al. (2013)	Spain	3/0	t073, t002, t711	ST45, ST5, ST2176	CC45, CC5, CC8	ND	ND	ND

Abbreviations: CC, clonal complex; ND, not detected; NR, not reported in detail; NT, not tested; ST, sequence type.

lineage that has no host specificity, as it has also been associated with rabbits, horses, cattle and swine (Alba et al., 2015; Feltrin et al., 2016; Islam et al., 2017; Silva et al., 2020). Conversely, MRSA-CC1 has often been linked to hospital-associated outbreaks, especially in the intensive care unit (Monecke et al., 2020). The role of pets in the dissemination of *S. aureus*-CC1 isolates should be evaluated in the future.

The ST22 lineage is found in many of the MRSA isolates from dogs and it is known as a human epidemic clone (EMRSA-15) (Katakweba et al., 2016). The EMRSA-15 (ST22) is predominantly a pandemic MRSA isolated both in hospital and community settings. It was estimated that ~98% of all ST22 isolates reported in the literature have been associated with humans (Roberts et al., 2018). However, this ST has previously been isolated from dogs in other geographical regions, supporting the notion that this *S. aureus* lineage may have adapted to the canine host (Katakweba et al., 2016). Nevertheless, this clone may be of human origin and transmitted to dogs in the household environment. The other predominant lineage detected among MRSA from dogs was ST36, which is one of the three pandemic lineages that have been described within CC30 causing epidemic waves (Di Gregorio et al., 2021). Moreover, MRSA isolates of the genetic lineages ST5 and ST93 were also reported in nasal strains from healthy dogs in Australia (Ma, Worthing, Ward, et al., 2020).

In cats, MRSA isolates belonging to ST80, ST30, ST496, ST749, ST71, ST316, ST84 and CC22 genetic lineages were identified in four of the eligible studies (Elmoslemany et al., 2021; Loeffler et al., 2011; Quitoco et al., 2013; Rynhoud et al., 2021). In relation to nasal MSSA of healthy cats' samples, only two eligible studies carried out the molecular typing of isolates with the detection of lineages CC5, CC15, CC45 and CC8 (Gharsa, Ben Slama, et al., 2015; Gómez-Sanz, Torres, Benito, et al., 2013) (Table 4). It is interesting to note that the genetic lineage CC22, often considered HA-MRSA, and a frequent lineage in dogs was in addition detected in one study on healthy cats (Loeffler et al., 2011).

The definition of community- and hospital-associated strains is no longer a strict one, as CA-MRSA strains have been described to be responsible for outbreaks in hospital settings, while HA-MRSA strains have been reported spreading in the community (Bal et al., 2016; Coll et al., 2017). However, it is crucial to delineate the pattern of predominant transmission and degree of spillover from community to hospital and vice-versa. The ability of MRSA-ST80 to disseminate at the community level has been reported (Drougka et al., 2016; Mairi et al., 2020). Furthermore, the transmission of MRSA-ST80 among different host species in the context of households and veterinary practices has been described by Drougka et al. (2016),

who reported that dogs and cats can be the reservoir of MRSA-ST80 which can cause severe infection in humans. The so-called paediatric clone, CC5, has globally been associated with community outbreaks (McManus et al., 2021).

Genetic lineages associated with *S. pseudintermedius* isolates from the nasal cavities of healthy dogs and cats

Out of the eight studies with molecular typing on *S. pseudintermedius* in healthy dogs, a great diversity of lineages was reported among MSSP isolates, and no specific predominance was observed (Table 5). As observed in the current review, high MLST clonal diversity is a common characteristic of MSSP (Pires Dos Santos et al., 2016). The diverse global population structures of *S. pseudintermedius* are evident in the world map comparing shared STs (Perreten et al., 2010).

Moreover, diverse lineages were also detected among MRSP of healthy dogs, although ST71 lineage was predominant (14.6% of isolates), detected in studies carried out in Spain, Brazil and Australia (Table 5). MRSP isolates of the lineage ST71 have largely been associated with sick dogs. Although the ST71 was considered a major MRSP-clone in Europe, recent studies have reported a downward trend in the prevalence of the MRSP-ST71 lineage among companion animals in France, Netherlands and Finland (Bergot et al., 2018; Duim et al., 2016; Grönthal et al., 2017). In relation to MRSP-ST71 from nasal swabs of healthy cats and dogs, other non-European countries have reported this clone, such as Australia (Rynhoud et al., 2021). It could be that veterinary personnel acted as carriers and facilitated the transmission of the MRSP-ST71 clone between animals they handle, or pet owners who interact with other dogs in the community such as in dogs' parks. The MRSP-ST71 has already been incriminated in potential zoonotic diseases (Kitagawa et al., 2021), reflecting the recent emergence of these important multidrug-resistant bacteria in animal and public health. Conversely, the other clone of high relevance, especially in the USA, MRSP-ST68, was not reported from nasal cavities of healthy dogs and cats in the studies included in this systematic review.

Although none of the MRSP isolates from cats was genetically characterized, an MSSP isolate was found to be ST142 by Gómez-Sanz, Torres, Lozano, et al. (2013) (Table 5). Although the MSSP-ST142 is a rarely reported lineage in cats, it has been detected in household dogs, and their owner; and could represent a case of transmission between dogs and cats in the same household

TABLE 5 Molecular typing reports of *Staphylococcus pseudintermedius* isolated from the nasal cavities of healthy dogs and cats

Reference	Country	No. of <i>S. pseudintermedius</i> /no. of MRSP	Molecular typing of MSSP (no. of isolates, when available)		Molecular typing of MRSP isolates (no. of isolates, when available)	
			ST	CC	ST	CC
<i>Healthy dog population</i>						
Gharsa et al. (2013)	Tunisia	55/0	ST20, ST44, ST69, ST70, ST78, ST100, ST108, ST160, ST161, ST162	NT	NT	ND
Abouelkhair et al. (2018)	Botswana	3/0	ST887, ST888, ST889	NT	NT	NT
Quitoco et al. (2013)	Brazil	0/1	NT	NT	ST71	NT
Penna et al. (2021)	Brazil	NT/3	NT	NT	ST30 (3)	NT
Rynhoud et al. (2021)	Australia	NT/7	NT	NT	ST496, ST749, ST71, ST316, ST84	NT
Gómez-Sanz, Torres, Benito, et al. (2013)	Spain	14/2	ST42, ST141, ST154, ST33, ST142, ST29, ST7, ST77	NT	ST71, ST92	NT
Gómez-Sanz, Torres, Lozano, et al. (2013)	Spain	22/8	ST20, ST31, ST44, ST160, ST181, ST182, ST183, ST184, ST185, SST186, ST187, ST188, ST190	NT	ST71 (2)	NT
<i>Healthy cat population</i>						
Gómez-Sanz, Torres, Lozano, et al. (2013)	Spain	1/0	ST142	NT	NT	ND

Abbreviations: CC, clonal complex; ND, not detected; NR, not reported in detail; NT, not tested; ST, sequence type.

TABLE 6 Characteristics of *Staphylococcus aureus* isolates carrying key virulence factors identified from the nasal cavities of healthy dogs and cats

Reference	Country/subjects	Sample size	spa type/ST/CC of positive isolates (no. of isolates)	Virulence gene identified	Methicillin susceptibility (no. of isolates)
Wachtmeister (2018)	Uganda/dogs	39	NT (1)	<i>luk-S/F-PV</i>	MRSA (1)
Penna et al. (2021)	Brazil/dogs	88	ST30 (3)	<i>luk-S/F-PV</i>	MRSA (3)
Ma, Worthing, Gottlieb, et al. (2020)	Australia/dogs	303	ST5 (1), ST93 (3)	<i>luk-S/F-PV</i>	MRSA (4)
Gómez-Sanz, Torres, Lozano, et al. (2013)	Spain/dogs	54	t209/ST109/CC9 (1)	<i>eta</i>	MSSA (1)
Gómez-Sanz, Torres, Lozano, et al. (2013)	Spain/dogs	54	t159/ST121/CC121 (1)	<i>etb</i>	MSSA (1)
Wedley et al. (2014)	UK/dogs	724	t1062 (1), t601 (1)	<i>eta</i>	MSSA (2)
Wedley et al. (2014)	UK/dogs	724	t660 (1), t601 (1)	<i>etd</i>	MSSA (2)
Wedley et al. (2014)	UK/dogs	724	t022 (1)	<i>tst</i>	MRSA (1)
Elmoslemany et al. (2021)	Saudi Arabia/cats	209	ST80 (1)	<i>luk-S/F-PV</i>	MRSA (1)

Abbreviations: CC, clonal complex; NT, not tested; ST, sequence type.

(Gómez-Sanz, Torres, Lozano, et al., 2013; Gómez-Sanz et al., 2019).

Major virulence factors of *S. aureus* detected from nasal cavities of healthy dogs and cats

Genes of several virulence factors including leukotoxins, enterotoxins and exfoliatins were reported in some of the reviewed and eligible studies of healthy dogs and cats (Table 6).

Eight MRSA strains carrying *luk-S/F-PV*, three MSSA *eta*-positive, one MSSA *etb*-positive, two MSSA *etd*-positive and one MRSA *tst*-positive were reported in five studies on healthy dogs. However, only one MRSA *luk-S/F-PV*-positive strain (of the lineage ST80) was detected in one study on healthy cats (Elmoslemany et al., 2021). Previous results have shown that *luk-S/F-PV* (encoding the Panton-Valentine Leucocidin, PVL) is considered a stable genetic marker for CA-MRSA and has been associated with necrotic skin lesions and necrotic pneumonia (Kong et al., 2016; Labandeira-Rey et al., 2007; Shallcross et al., 2013). The *luk-S/F-PV* gene was detected in three studies on healthy dogs; in one of them, three PVL-positive MRSA-ST30 isolates were reported in Brazil (Penna et al., 2021). Another study from Australia demonstrated MRSA-*luk-S/F-PV* in 4 out of 5 strains (3 ST93 and 1 ST5) from healthy dogs (Ma, Worthing, Ward, et al., 2020). However, the genetic lineage of the MRSA-*luk-S/F-PV*-positive strain from the study of Wachtmeister (2018) was not determined. Moreover, one MRSA-*tst*-positive strain (*spa*-type t022) was detected in a healthy dog in the United Kingdom (Wedley et al., 2014).

Major virulence factors of *S. pseudintermedius* detected from nasal cavities of healthy dogs and cats

Most of the *S. pseudintermedius* isolates in which virulence was analysed, carried a diverse range of virulence factors that are responsible for host-specific clinical symptoms such as the pyodermic infection on dogs and cats (Table 7). The *lukS/F-I*, *siet*, *expA* genes were particularly often detected in nasal *S. pseudintermedius* isolates. MSSP-*lukS/F-I* positive isolates were reported in three studies involving dogs and cats (Gharsa et al., 2013; Gómez-Sanz, Torres, Benito, et al., 2013; Gómez-Sanz, Torres, Lozano, et al., 2013). Similarly, *siet*-carrying *S. pseudintermedius* isolates were detected in eight studies on healthy dogs and cats. Moreover, staphylococcal enterotoxins genes (*sea*, *seb*, *sec*, *sed*, *sei*, *sej*, *sek* and *ser*) were also reported in some studies (Table 7).

TABLE 7 Characteristics of *Staphylococcus pseudintermedius* isolates carrying key virulence factors identified from the nasal cavities of healthy dogs and cats

Reference	Country/subjects	Sample size	No. of <i>S. pseudintermedius</i> (%) / MRSP (%)	Virulence genes identified
Moses et al. (2020)	Nigeria/dogs	35	25 (71.4)/18 (51.1)	<i>luk-D, siet, sec, exi</i>
Gharsa et al. (2013)	Tunisia/dogs	100	55 (55.0)/0 (0.0)	<i>luk-S/F-I, expA, se-int, seccanine, siet, sea, seb, sec, sed, sei, sej, sek, ser, hlgv</i>
Han et al. (2015)	South Korea/dogs	92	32 (34.8)/22 (23.9)	<i>icaA, icaD</i>
Han et al. (2016)	Korea/dogs	119	29 (24.7)/21 (17.6)	<i>siet, sea</i>
Rynhoud et al. (2021)	Australia/dogs	61	NT/7 (11.5)	<i>lukF-P, srrA, clpX, coa, ebpS, hrtA, lip, sarA, sarR, sarZ, siet, speta, spsA, spsB, spsC, spsE, spsG, spsH, spsK, spsM, spsN, spsR, hlgB, clpP</i>
Gómez-Sanz et al. (2011)	Spain/dogs	196	NR/9 (4.6)	<i>hlg-v, lukS-I, lukF-I, siet, si-ent</i>
Gómez-Sanz, Torres, Lozano, et al. (2013)	Spain/dogs	54	14 (25.9)/2 (3.7)	<i>luk-S/F-I, siet, expA</i>
Gómez-Sanz, Torres, Benito, et al. (2013)	Spain/dogs	98	22 (22.4)/8 (8.2)	<i>luk-S/F-I</i>
Wedley et al. (2014)	UK/dogs	724	80 (11.0)/0 (0.0)	<i>seG, seI, seM, seN, seO, seU, lukDE, etA, etD</i>
Rynhoud et al. (2021)	Australia/cats	127	NT/9 (7.1)	<i>lukF-P, srrA, clpX, coa, ebpS, hrtA, lip, sarA, sarR, sarZ, siet, speta, spsA, spsB, spsC, spsE, spsG, spsH, spsK, spsM, spsN, spsR, hlgB, clpP</i>
Gómez-Sanz, Torres, Lozano, et al. (2013)	Spain/cats	12	1 (8.3)/0 (0.0)	<i>luk-S/F-I, siet, hla, hld, se-int</i>

Abbreviation: NT, not tested.

Biofilms produced by *S. pseudintermedius* play an important role in the pathophysiology of infection and colonization (Jain & Agarwal, 2009; Singh et al., 2013). Some studies reported that MRSP-ST71 can produce biofilms, suggesting the necessity of investigating the prevalence of biofilm-producing *S. pseudintermedius* and their implications on AMR in veterinary medical practices (Dicicco et al., 2012; Osland et al., 2012; Singh et al., 2013). The *icaA* and *icaD* genes responsible for biofilm production were detected among healthy dogs' isolates in one study (Han et al., 2015).

Host adaptation system of *S. aureus* isolates from nasal cavities of healthy dogs and cats

In relation to the host adaptation system of *S. aureus* for humans, the immune evasion cluster (IEC) harbours the gene *scn* (a marker of the IEC system) as well as different combinations of the *sak*, *chp* and *sea* (or *sep*) genes (Ahmadrajab et al., 2017; Gómez et al., 2021). These genes

encode staphylococcal complement inhibitor (encoded by *scn* gene), staphylokinase (SAK), chemotaxis inhibitory protein (CHP) and staphylococcal enterotoxin A (SEA). It is important to remark that IEC genes are bacteriophage encoded (Ahmadrajab et al., 2017) and their presence (with *scn* gene as a marker) is considered a human-adaptation marker (Gómez et al., 2021). The IEC system was rarely investigated on *S. aureus* isolates from healthy dogs and cats (just two of the eligible studies). In the study of Gómez-Sanz, Torres, Benito, et al. (2013) on dogs and cats, 54.2% of the *S. aureus* isolates (all MSSA) were *scn*-positive, and they presented the IEC-types B, C and E, and corresponded to the genetic lineages CC5, CC45, CC22 and CC88. These data infer that more than half of the MSSA isolates of dog origin contained the human adaptation marker. In the other study on healthy dogs by Ma, Worthing, Gottlieb, et al. (2020), four out of the five MRSA strains (of the genetic lineages ST5 and ST93) were IEC type B, while the remaining one was IEC type A (ST1). A suitable explanation for these findings is that the isolates are most likely from community transmission and/or the dogs-owners. Also, all the five MRSA strains isolated

from the nasal samples of healthy dogs in the study of Ma, Worthing, Gottlieb, et al. (2020) were *scn*-positive.

As a limitation of this study, analysis of global data was performed using studies from low-resources and developed countries, that used different techniques for bacterial isolation and identification. The studies' methodologies differences might to some extent affect the prevalence values of *S. aureus* or *S. pseudintermedius* reported in healthy dogs and cats. Consequently, the pooled prevalence data obtained could be misreported (i.e. under-reported or over-reported).

CONCLUSION

It can be inferred that the nasal carriage of *S. aureus* and *S. pseudintermedius* in healthy dogs were moderate (10.9% and 18.3%) but low in healthy cats (3.2% and 1.2%). However, the nasal carriage of MRSA and MRSP in both healthy dogs and cats was low (<3.5%). Moreover, a high diversity of lineages and clones was detected in both staphylococcal species, especially among MSSP and MSSA. The MRSA strains recovered from healthy dogs and cats frequently belonged to human-associated genetic lineages which indicates the transmission of these clones within the household niche. Conversely, the MSSA strains corresponded to genetic lineages associated with both humans and animals. Both *S. aureus* and *S. pseudintermedius* showed high levels of AMR to commonly used human antibiotics. MRSP isolates from dogs and cats showed more frequently a MDR phenotype than MRSA. Moreover, some *S. aureus* isolates carried virulence factors of human health importance, as is the case of *luk-S/F-PV*, *tst*, *eta*, *etb* and *etd*. It is necessary to implement adequate epidemiological and microbiological surveillance on *S. aureus/S. pseudintermedius* and MRSA/MRSP in companion animals. Additional studies should include follow-up of molecular characterization of isolates from countries with under-studied nasal staphylococci isolates. By extension, studies should be more tailored towards the 'One Health' approach (humans-animals-and their shared environment).

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CONFLICT OF INTEREST

No conflict of interest declared.

DATA AVAILABILITY STATEMENT

The data extracted and utilized for this study have been thoroughly referenced. However, data related to the statistical analyses can be made available on request through the corresponding author (C.T.)

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REFERENCES

- Abdel-Moein, K.A., El-Hariri, M. & Samir, A. (2012) Methicillin-resistant *Staphylococcus aureus*: an emerging pathogen of pets in Egypt with a public health burden: MRSA infection in pets: an emerging zoonosis in Egypt. *Transboundary and Emerging Diseases*, 59, 331–335.
- Abdullahi, I.N., Lozano, C., Ruiz-Ripa, L., Fernández-Fernández, R., Zarazaga, M. & Torres, C. (2021) Ecology and genetic lineages of nasal *Staphylococcus aureus* and MRSA carriage in healthy persons with or without animal-related occupational risks of colonisation: a review of global reports. *Pathogens*, 10, 1000. <https://doi.org/10.3390/pathogens10081000>
- Abdullahi, I.N., Fernández-Fernández, R., Juárez-Fernández, G., Martínez-Álvarez, S., Eguizábal, P., Zarazaga, M. et al. (2021) Wild animals are reservoirs and sentinels of *Staphylococcus aureus* and MRSA clones: a problem with "one health" concern. *Antibiotics*, 10(12), 1556. <https://doi.org/10.3390/antibiotic10121556>
- Abouelkhair, M.A., Thompson, R., Riley, M.C., Bemis, D.A. & Kania, S.A. (2018) Complete genome sequences of three *Staphylococcus pseudintermedius* strains isolated from Botswana. *Genome Announcements*, 6, e01599-17. <https://doi.org/10.1128/genomE.A.01599-17>
- Ahmadrajabi, R., Layegh-Khavidaki, S., Kalantar-Neyestanaki, D. & Fasihi, Y. (2017) Molecular analysis of immune evasion cluster (IEC) genes and intercellular adhesion gene cluster (ICA) among methicillin-resistant and methicillin-sensitive isolates of *Staphylococcus aureus*. *Journal of Preventive Medicine and Hygiene*, 58, E308–E314. <https://doi.org/10.15167/2421-4248/jpmh2017.58.4.711>
- Aires-de-Sousa, M. (2017) Methicillin-resistant *Staphylococcus aureus* among animals: current overview. *Clinical Microbiology and Infection*, 23(6), 373–380. <https://doi.org/10.1016/j.cmi.2016.11.002>
- Alba, P., Feltrin, F., Cordaro, G., Porrero, M.C., Kraushaar, B., Argudín, M.A. et al. (2015) Livestock-associated methicillin resistant and methicillin susceptible *Staphylococcus aureus* sequence type (CC)1 in European farmed animals: high genetic relatedness of isolates from Italian cattle herds and humans. *PLoS One*, 10, e0137143. <https://doi.org/10.1371/journal.pone.0137143>
- Bal, A.M., Coombs, G.W., Holden, M.T.G., Lindsay, J.A., Nimmo, G.R., Tattevin, P. et al. (2016) Genomic insights into the emergence and spread of international clones of healthcare-, community- and livestock-associated methicillin-resistant *Staphylococcus aureus*: blurring of the traditional definitions.

- Journal of Global Antimicrobial Resistance*, 6, 95–101. <https://doi.org/10.1016/j.jgar.2016.04.004>
- Bannoehr, J. & Guardabassi, L. (2012) *Staphylococcus pseudintermedius* in the dog: taxonomy, diagnostics, ecology, epidemiology and pathogenicity. *Veterinary Dermatology*, 23(4), 253–e52. <https://doi.org/10.1111/j.1365-3164.2012.01046.x>
- Bean, D.C. & Wigmore, S.M. (2016) Carriage rate and antibiotic susceptibility of coagulase-positive staphylococci isolated from healthy dogs in Victoria, Australia. *Australian Veterinary Journal*, 94(12), 456–460. <https://doi.org/10.1111/avj.12528>
- Benito, D., Lozano, C., Rezusta, A., Ferrer, I., Vasquez, M.A., Ceballos, S. et al. (2014) Characterisation of tetracycline and methicillin resistant *Staphylococcus aureus* strains in a Spanish hospital: is livestock-contact a risk factor in infections caused by MRSA CC398? *International Journal of Medical Microbiology*, 304, 1226–1232. <https://doi.org/10.1016/j.ijmm.2014.09.004>
- Bergot, M., Martins-Simoes, P., Kilian, H., Châtre, P., Worthing, K.A., Norris, J.M. et al. (2018) Evolution of the population structure of *Staphylococcus pseudintermedius* in France. *Frontiers in Microbiology*, 9, 3055. <https://doi.org/10.3389/fmicb.2018.03055>
- Bierowiec, K., Miszczak, M., Korzeniowska-Kowal, A., Wzorek, A., Płókarz, D. & Gamian, A. (2021) Epidemiology of *Staphylococcus pseudintermedius* in cats in Poland. *Scientific Reports*, 11(1), 18898. <https://doi.org/10.1038/s41598-021-97976-z>
- Boost, M.V., O'Donoghue, M.M. & Siu, K.H.G. (2007) Characterisation of methicillin-resistant *Staphylococcus aureus* isolates from dogs and their owners. *Clinical Microbiology and Infection*, 13, 731–733.
- Börjesson, S., Gómez-Sanz, E., Ekström, K., Torres, C. & Grönlund, U. (2015) *Staphylococcus pseudintermedius* can be misdiagnosed as *Staphylococcus aureus* in humans with dog bite wounds. *European Journal of Clinical Microbiology & Infectious Diseases*, 34(4), 839–844. <https://doi.org/10.1007/s10096-014-2300-y>
- Carroll, K.C., Burnham, C.D. & Westblade, L.F. (2021) From canines to humans: clinical importance of *Staphylococcus pseudintermedius*. *PLoS Pathogens*, 17(12), e1009961. <https://doi.org/10.1371/journal.ppat.1009961>
- Ceballos, S., Aspiroz, C., Ruiz-Ripa, L., Zarazaga, M., Torres, C. & Spanish Study Group on Clinical LA-MRSA. (2020) Antimicrobial resistance phenotypes and genotypes of methicillin-resistant *Staphylococcus aureus* CC398 isolates from Spanish hospitals. *International Journal of Antimicrobial Agents*, 55, 105907. <https://doi.org/10.1016/j.ijantimicag.2020.105907>
- Chanachithong, P. & Prapasarakul, N. (2011) Biochemical markers and protein pattern analysis for canine coagulase-positive staphylococci and their distribution on dog skin. *Journal of Microbiological Methods*, 86, 175–181.
- Chueahiran, S., Yindee, J., Boonkham, P., Suanpairintr, N. & Chanachithong, P. (2021) Methicillin-resistant *Staphylococcus aureus* clonal complex 398 as a major MRSA lineage in dogs and cats in Thailand. *Antibiotics*, 10(3), 243. <https://doi.org/10.3390/antibiotics10030243>
- Chasioti, M., Petinaki, E., Sarrou, S., Zafeiriou, E. & Roussaki-Schulze, A. (2019) Prevalence and colonisation of *S. aureus* in nasal cavity of domestic animals and of those who are taking care of them. *Animal Husbandry, Dairy and Veterinary Science*. *Animal Husbandry and Dairy Veterinary Science*, 3, 1–5. <https://doi.org/10.15761/AHDVS.1000169>
- Coelho, C., Torres, C., Radhouani, H., Pinto, L., Lozano, C., Gómez-Sanz, E. et al. (2011) Molecular detection and characterisation of methicillin-resistant *Staphylococcus aureus* (MRSA) isolates from dogs in Portugal. *Microbial Drug Resistance*, 17, 333–337.
- Coll, F., Harrison, E.M., Toleman, M.S., Reuter, S., Raven, K.E., Blane, B. et al. (2017) Longitudinal genomic surveillance of MRSA in the UK reveals transmission patterns in hospitals and the community. *Science and Translational Medicine*, 9, eaak9745. <https://doi.org/10.1126/scitranslmed.aak9745>
- Collignon, P. & Voss, A. (2015) China, what antibiotics and what volumes are used in food production animals? *Antimicrobial Resistance and Infectious Control*, 16. <https://doi.org/10.1186/s13756-015-0056-5>
- Dafale, N.A., Srivastava, S. & Purohit, H.J. (2020) Zoonosis: an emerging link to antibiotic resistance under "one health approach". *Indian Journal of Microbiology*, 60(2), 139–152. <https://doi.org/10.1007/s12088-020-00860-z>
- Daodu, O.B., Amosun, E.A. & Oluwayelu, D.O. (2016) Antibiotic resistance profiling and microbiota of the upper respiratory tract of apparently healthy dogs in Ibadan, southwest, Nigeria. *African Journal of Infectious Diseases*, 11, 1–11.
- Decline, V., Effendi, M.H., Rahmaniar, R.P., Yanestria, S.M. & Harijani, N. (2020) Profile of antibiotic-resistant and presence of methicillin-resistant *Staphylococcus aureus* from nasal swab of dogs from several animal clinics in Surabaya, Indonesia. *International Journal of One Health*, 6, 90–94.
- Devriese, L.A., Vancanneyt, M., Baele, M., Vaneechoutte, M., De Graef, E., Snauwaert, C. et al. (2005) *Staphylococcus pseudintermedius* sp. nov., a coagulase-positive species from animals. *International Journal of Systematic and Evolutionary Microbiology*, 55(Pt 4), 1569–1573. <https://doi.org/10.1099/ijs.0.63413-0>
- Di Gregorio, S., Haim, M.S., Vielma Vallenilla, J., Cohen, V., Rago, L., Gulone, L. et al. (2021) Genomic epidemiology of CC30 methicillin-resistant *Staphylococcus aureus* strains from Argentina reveals four major clades with distinctive genetic features. *MSphere*, 6, e01297-20. <https://doi.org/10.1128/mSphere.01297-20>
- Dicicco, M., Neethirajan, S., Singh, A. & Weese, J.S. (2012) Efficacy of clarithromycin on biofilm formation of methicillin-resistant *Staphylococcus pseudintermedius*. *BMC Veterinary Research*, 8, 225. <https://doi.org/10.1186/1746-6148-8-225>
- Drougka, E., Foka, A., Koutinas, C.K., Jelastopulu, E., Giormezis, N., Farmaki, O. et al. (2016) Interspecies spread of *Staphylococcus aureus* clones among companion animals and human close contacts in a veterinary teaching hospital. A cross-sectional study in Greece. *Preventive Veterinary Medicine*, 126, 190–198.
- Duim, B., Verstappen, K.M., Broens, E.M., Laarhoven, L.M., van Duijkeren, E., Hordijk, J. et al. (2016) Changes in the population of methicillin-resistant *Staphylococcus pseudintermedius* and dissemination of antimicrobial-resistant phenotypes in The Netherlands. *Journal of Clinical Microbiology*, 54, 283–288.
- Elmoslemany, A., Elsohaby, I., Alorabi, M., Alkafafy, M., Al-Marri, T., Aldoweriej, A. et al. (2021) Diversity and risk factors associated with multidrug and methicillin-resistant staphylococci isolated from cats admitted to a veterinary clinic in Eastern Province, Saudi Arabia. *Antibiotics*, 10, 367.
- Elnageh, H.R., Hiblu, M.A., Abbassi, M.S., Abouzeed, Y.M. & Ahmed, M.O. (2021) Prevalence and antimicrobial resistance of *Staphylococcus* species isolated from cats and dogs. *Open Veterinary Journal*, 10, 452–456.

- Elshabrawy, M.A., Abouelhag, H.A., Khairy, E.A., Marie, H.S. & Hakim, A.S. (2020) Molecular divergence of *Staphylococcus aureus* isolated from dogs and cats. Available from: <http://jjbs.hu.edu.jo/files/vol13/n2/Paper%20Number%203.pdf> [Accessed 22nd October 2015].
- Epstein, C.R., Yam, W.C., Peiris, J.S.M. & Epstein, R.J. (2009) Methicillin-resistant commensal staphylococci in healthy dogs as a potential zoonotic reservoir for community-acquired antibiotic resistance. *Infection, Genetics and Evolution*, 9, 283–285.
- Espinosa-Gongora, C., Chrobak, D., Moodley, A., Bertelsen, M.F. & Guardabassi, L. (2012) Occurrence and distribution of *Staphylococcus aureus* lineages among zoo animals. *Veterinary Microbiology*, 158, 228–231. <https://doi.org/10.1016/j.vetmic.2012.01.027>
- Fabri, F.V., Pinto, N.B., de Mattos, M.S.F., Rodrigues, R.F., Shinohara, D.R., Pereira, P.M. et al. (2021) First report of oxacillin-susceptible *mecA*-positive *Staphylococcus aureus* in healthy dogs and their owners in southern Brazil. *Preventive Veterinary Medicine*, 189, 105286.
- Feltrin, F., Alba, P., Kraushaar, B., Ianzano, A., Argudín, M.A., Di Matteo, P. et al. (2016) A livestock-associated, multidrug-resistant, methicillin-resistant *Staphylococcus aureus* clonal complex 97 lineage spreading in dairy cattle and pigs in Italy. *Applied and Environmental Microbiology*, 82, 816–821.
- Fletcher, S. (2015) Understanding the contribution of environmental factors in the spread of antimicrobial resistance. *Environmental Health and Preventive Medicine*, 20(4), 243–252. <https://doi.org/10.1007/s12199-015-0468-0>
- Garbacz, K., Żarnowska, S., Piechowicz, L. & Haras, K. (2013) Staphylococci isolated from carriage sites and infected sites of dogs as a reservoir of multidrug resistance and methicillin resistance. *Current Microbiology*, 66, 169–173.
- Gharsa, H., Ben Slama, K., Gómez-Sanz, E., Lozano, C., Klibi, N., Jouini, A. et al. (2013) Antimicrobial resistance, virulence genes, and genetic lineages of *Staphylococcus pseudintermedius* in healthy dogs in Tunisia. *Microbial Ecology*, 66, 363–368.
- Gharsa, H., Ben Slama, K., Gómez-Sanz, E., Lozano, C., Zarazaga, M., Messadi, L. et al. (2015) Molecular characterisation of *Staphylococcus aureus* from nasal samples of healthy farm animals and pets in Tunisia. *Vector-Borne and Zoonotic Diseases*, 15, 109–115.
- Gharsa, H., Slama, K.B., Gómez-Sanz, E., Gómez, P., Klibi, N., Zarazaga, M. et al. (2015) Characterisation of nasal *Staphylococcus delphini* and *Staphylococcus pseudintermedius* isolates from healthy donkeys in Tunisia. *Equine Veterinary Journal*, 47, 463–436.
- Gingrich, E.N., Kurt, T., Hyatt, D.R., Lappin, M.R. & Ruch-Gallie, R. (2011) Prevalence of methicillin-resistant staphylococci in northern Colorado shelter animals. *Journal of Veterinary Diagnostic Investigation*, 23, 947–950.
- Gómez, P., Lozano, C., Camacho, M.C., Lima-Barbero, J.F., Hernández, J.M., Zarazaga, M. et al. (2016) Detection of MRSA ST3061-t843-*mecC* and ST398-t011-*mecA* in white stork nestlings exposed to human residues. *Journal of Antimicrobial Chemotherapy*, 71, 53–57. <https://doi.org/10.1093/jac/dkv314>
- Gómez, P., Ruiz-Ripa, L., Fernández-Fernández, R., Gharsa, H., Ben Slama, K., Höfle, U. et al. (2021) Genomic analysis of *Staphylococcus aureus* of the lineage CC130, including *mecC*-carrying MRSA and MSSA isolates recovered of animal, human, and environmental origins. *Frontiers in Microbiology*, 12, 655994.
- Gómez-Sanz, E., Ceballos, S., Ruiz-Ripa, L., Zarazaga, M. & Torres, C. (2019) Clonally diverse methicillin and multidrug resistant coagulase negative staphylococci are ubiquitous and pose transfer ability between pets and their owners. *Frontiers in Microbiology*, 10, 485.
- Gómez-Sanz, E., Torres, C., Benito, D., Lozano, C. & Zarazaga, M. (2013) Animal and human *Staphylococcus aureus* associated clonal lineages and high rate of *Staphylococcus pseudintermedius* novel lineages in Spanish kennel dogs: predominance of *S. aureus* ST398. *Veterinary Microbiology*, 166, 580–589.
- Gómez-Sanz, E., Torres, C., Lozano, C. & Zarazaga, M. (2013) High diversity of *Staphylococcus aureus* and *Staphylococcus pseudintermedius* lineages and toxigenic traits in healthy pet-owning household members. Underestimating normal household contact? *Comparative Immunology, Microbiology and Infectious Diseases*, 36, 83–94.
- Gómez-Sanz, E., Torres, C., Lozano, C., Sáenz, Y. & Zarazaga, M. (2011) Detection and characterisation of methicillin-resistant *Staphylococcus pseudintermedius* in healthy dogs in La Rioja, Spain. *Comparative Immunology, Microbiology and Infectious Diseases*, 34, 447–453.
- Grönthal, T., Eklund, M., Thomson, K., Piiparinen, H., Sironen, T. & Rantala, M. (2017) Antimicrobial resistance in *Staphylococcus pseudintermedius* and the molecular epidemiology of methicillin-resistant *S. pseudintermedius* in small animals in Finland. *The Journal of Antimicrobial Chemotherapy*, 72, 1021–1030. <https://doi.org/10.1093/jac/dkw559>
- Guinane, C.M., Ben Zakour, N.L., Tormo-Mas, M.A., Weinert, L.A., Lowder, B.V., Cartwright, R.A. et al. (2010) Evolutionary genomics of *Staphylococcus aureus* reveals insights into the origin and molecular basis of ruminant host adaptation. *Genome Biological Evolution*, 2, 454–466. <https://doi.org/10.1093/gbe/evq031>
- Hakim, H., Jit, P., Asha, K., Vergis, J., Deepa, P.M., Suma, N. et al. (2019) Nasal carriage of *Staphylococcus aureus* and MRSA among companion animals and livestock in wayanad district, India. *International Journal of Current Microbiology and Applied Sciences*, 8, 1254–1260.
- Han, J.-I., Yang, C.-H. & Park, H.-M. (2015) Emergence of biofilm-producing *Staphylococcus pseudintermedius* isolated from healthy dogs in South Korea. *The Veterinary Quarterly*, 35, 207–210.
- Han, J.-I., Yang, C.-H. & Park, H.-M. (2016) Prevalence and risk factors of *Staphylococcus* spp. carriage among dogs and their owners: a cross-sectional study. *Veterinary Journal*, 212, 15–21.
- Islam, M.Z., Espinosa-Gongora, C., Damborg, P., Sieber, R.N., Munk, R., Husted, L. et al. (2017) Horses in Denmark are a reservoir of diverse clones of methicillin-resistant and -susceptible *Staphylococcus aureus*. *Frontiers in Microbiology*, 8, 543.
- Jain, A. & Agarwal, A. (2009) Biofilm production, a marker of pathogenic potential of colonising and commensal staphylococci. *Journal of Microbiological Methods*, 76, 88–92.
- Katakweba, A.S., Muhairwa, A.P., Espinosa-Gongora, C., Guardabassi, L., Mtambo, M.M.A. & Olsen, J.E. (2016) *spa* typing and antimicrobial resistance of *Staphylococcus aureus* from

- healthy humans, pigs and dogs in Tanzania. *Journal of Infection in Developing Countries*, 10, 143–148.
- Kitagawa, H., Hisatsune, J., Ohge, H., Kutsuno, S., Hara, T., Masuda, K. et al. (2021) Implanted port catheter system infection caused by methicillin-resistant *Staphylococcus pseudintermedius* ST71-SCCmec type III. *Internal Medicine*, 60, 2337–2340.
- Kong, E.F., Johnson, J.K. & Jabra-Rizk, M.A. (2016) Community-associated methicillin-resistant *Staphylococcus aureus*: an enemy amidst us. *PLoS Pathogens*, 12, e1005837.
- Labandeira-Rey, M., Couzon, F., Boisset, S., Brown, E.L., Bes, M., Benito, Y. et al. (2007) *Staphylococcus aureus* Panton-Valentine Leukocidin causes necrotizing pneumonia. *Science*, 315, 1130–1133. <https://doi.org/10.1126/science.1137165>
- Loeffler, A., Pfeiffer, D.U., Lindsay, J.A., Soares Magalhães, R.J. & Lloyd, D.H. (2011) Prevalence of and risk factors for MRSA carriage in companion animals: a survey of dogs, cats and horses. *Epidemiology and Infection*, 139, 1019–1028.
- Loeffler, A., Pfeiffer, D.U., Lindsay, J.A., Soares-Magalhaes, R. & Lloyd, D.H. (2010) Lack of transmission of methicillin-resistant *Staphylococcus aureus* (MRSA) between apparently healthy dogs in a rescue kennel. *Veterinary Microbiology*, 141(1–2), 178–181. <https://doi.org/10.1016/j.vetmic.2009.08.001>
- Loncaric, I., Tichy, A., Handler, S., Szostak, M.P., Tickert, M., Diab-Elshahawi, M. et al. (2019) Prevalence of methicillin-resistant *Staphylococcus* sp. (MRS) in different companion animals and determination of risk factors for colonisation with MRS. *Antibiotics*, 8, 36.
- Lord, J., Millis, N., Jones, R.D., Johnson, B., Kania, S.A. & Odoi, A. (2022) Patterns of antimicrobial, multidrug and methicillin resistance among *Staphylococcus* spp. isolated from canine specimens submitted to a diagnostic laboratory in Tennessee, USA: a descriptive study. *BMC Veterinary Research*, 18(1), 91. <https://doi.org/10.1186/s12917-022-03185-9>
- Lozano, C., Rezusta, A., Ferrer, I., Pérez-Laguna, V., Zarazaga, M., Ruiz-Ripa, L. et al. (2017) *Staphylococcus pseudintermedius* human infection cases in Spain: dog-to-human transmission. *Vector Borne Zoonotic Diseases*, 17, 268–270.
- Lynch, S.A. & Helbig, K.J. (2021) The complex diseases of *Staphylococcus pseudintermedius* in canines: where to next? *Veterinary Sciences*, 8(1), 11. <https://doi.org/10.3390/vetsc81010011>
- Ma, G.C., Worthing, K.A., Gottlieb, T., Ward, M.P. & Norris, J.M. (2020) Molecular characterisation of community-associated methicillin-resistant *Staphylococcus aureus* from pet dogs. *Zoonoses and Public Health*, 67(3), 222–230. <https://doi.org/10.1111/zph.12677>
- Ma, G.C., Worthing, K.A., Ward, M.P. & Norris, J.M. (2020) Commensal staphylococci including methicillin-resistant *Staphylococcus aureus* from dogs and cats in remote New South Wales, Australia. *Microbial Ecology*, 79(1), 164–174. <https://doi.org/10.1007/s00248-019-01382-y>
- Machado, A.B., Machado, M.F.R. & Picoli, S.U. (2017) An investigation of methicillin-resistant *Staphylococcus pseudintermedius* (MRSP) in domestic and shelter dogs in Montenegro (RS-Brazil). *Revista Brasileira de Saúde e Produção Animal/Brazilian Journal of Animal Health and Production*, 18, 542–548.
- Mairi, A., Touati, A. & Lavigne, J.-P. (2020) Methicillin-resistant *Staphylococcus aureus* ST80 clone: a systematic review. *Toxins*, 12, 119.
- Mališová, L., Šafránková, R., Kekláková, J., Petráš, P., Žemličková, H. & Jakubů, V. (2019) Correct specis identification (reclassification in CNCTC) of strains of *Staphylococcus intermedius*-group can improve an insight into their evolutionary history. *Folia Microbiologica*, 64, 231–236.
- Mama, O.M., Aspiroz, C., Lozano, C., Ruiz-Ripa, L., Azcona, J.M., Seral, C. et al. (2021) Penicillin susceptibility among invasive MSSA infections: a multicentre study in 16 Spanish hospitals. *The Journal of Antimicrobial Chemotherapy*, 76, 2519–2527.
- Mama, O.M., Aspiroz, C., Ruiz-Ripa, L., Ceballos, S., Iñiguez-Barrio, M., Cercenado, E. et al. (2021) Prevalence and genetic characteristics of *Staphylococcus aureus* CC398 isolates from invasive infections in Spanish Hospitals, focusing on the livestock-independent CC398-MSSA clade. *Frontiers in Microbiology*, 12, 623108. <https://doi.org/10.3389/fmicb.2021.623108>
- Mama, O.M., Ruiz-Ripa, L., Fernández-Fernández, R., González-Barrio, D., Ruiz-Fons, J.F. & Torres, C. (2019) High frequency of coagulase-positive staphylococci carriage in healthy wild boar with detection of MRSA of lineage ST398-t011. *FEMS Microbiology Letter*, 366, fny292.
- McManus, B.A., Aloba, B.K., Earls, M.R., Brennan, G.I., O'Connell, B., Monecke, S. et al. (2021) Multiple distinct outbreaks of Panton-valentine leukocidin-positive community-associated methicillin-resistant *Staphylococcus aureus* in Ireland investigated by whole-genome sequencing. *The Journal of Hospital Infection*, 108, 72–80.
- Mohamed, M.A., Aziz, S.A., Dhaliwal, G.K., Bejo, S.K., Nordin, M.L., Shaari, R. et al. (2020) Detection of *Staphylococcus pseudintermedius* in dogs and cats in Selangor, Malaysia. *American Journal of Animal and Veterinary Sciences*, 15, 10–14.
- Monecke, S., König, E., Earls, M.R., Leitner, E., Müller, E., Wagner, G.E. et al. (2020) An epidemic CC1-MRSA-IV clone yields false-negative test results in molecular MRSA identification assays: a note of caution, Austria, Germany, Ireland, 2020. *Eurosurveillance*, 25, 2000929.
- Moses, I.B., Esimone, C.O., Iroha, I.R., Ugbo, E.N., Nwuzo, A.C., Orji, J.O. et al. (2020) First report on the antibiotic resistance profiles and virulence genes of *Staphylococcus pseudintermedius* colonising dogs and humans in Abakaliki, south-East Nigeria. *Research Journal of Microbiology*, 15, 22–34.
- Murray, A.K., Lee, J., Bendall, R., Zhang, L., Sunde, M., Schau Slette-meås, J. et al. (2018) *Staphylococcus cornubiensis* sp. nov., a member of the *Staphylococcus intermedius* group (SIG). *International Journal of Systematic and Evolutionary Microbiology*, 68(11), 3404–3408. <https://doi.org/10.1099/ijsem.0.002992>
- Mustapha, M., Bukar-Kolo, Y.M., Geidam, Y.A. & Gulani, I.A. (2016) Phenotypic and genotypic detection of methicillin-resistant *Staphylococcus aureus* in hunting dogs in Maiduguri metropolitan, Borno state, Nigeria. *Veterinary World*, 9, 501–506.
- Myaing, T.T., Thaw, K.K., Htun, L.L., Mhon, M.M., Bawm, S., Linn, K.S. et al. (2016) Antimicrobial resistant pattern of methicillin-resistant *Staphylococcus aureus* isolated from stray dogs' nasal swabs to fifteen antimicrobials in Myanmar. *International Journal of Infectious Diseases*, 53, 48.
- Osland, A.M., Vestby, L.K., Fanuelson, H., Slette-meås, J.S. & Sunde, M. (2012) Clonal diversity and biofilm-forming ability of methicillin-resistant *Staphylococcus pseudintermedius*. *The Journal of Antimicrobial Chemotherapy*, 67(4), 841–848. <https://doi.org/10.1093/jac/dkr576>

- Papić, B., Golob, M., Zdovc, I., Kušar, D. & Avberšek, J. (2021) Genomic insights into the emergence and spread of methicillin-resistant *Staphylococcus pseudintermedius* in veterinary clinics. *Veterinary Microbiology*, 258, 109119. <https://doi.org/10.1016/j.vetmic.2021.109119>
- Paul, N.C., Bärghman, S.C., Moodley, A., Nielsen, S.S. & Guardabassi, L. (2012) *Staphylococcus pseudintermedius* colonisation patterns and strain diversity in healthy dogs: a cross-sectional and longitudinal study. *Veterinary Microbiology*, 160, 420–427.
- Penna, B., Silva, M.B., Soares, A.E.R., Vasconcelos, A.T.R., Ramundo, M.S., Ferreira, F.A. et al. (2021) Comparative genomics of MRSA strains from human and canine origins reveals similar virulence gene repertoire. *Scientific Reports*, 11, 4724.
- Perreten, V., Kadlec, K., Schwarz, S., Grönlund Andersson, U., Finn, M., Greko, C. et al. (2010) Clonal spread of methicillin-resistant *Staphylococcus pseudintermedius* in Europe and North America: an international multicentre study. *The Journal of Antimicrobial Chemotherapy*, 65(6), 1145–1154. <https://doi.org/10.1093/jac/dkq078>
- Perreten, V., Kania, S.A. & Bemis, D. (2020) *Staphylococcus ursi* sp. nov., a new member of the ‘*Staphylococcus intermedius* group’ isolated from healthy black bears. *International Journal of Systematic Evolutionary Microbiology*, 70, 4637–4645.
- Pires Dos Santos, T., Damborg, P., Moodley, A. & Guardabassi, L. (2016) Systematic review on global epidemiology of methicillin-resistant *Staphylococcus pseudintermedius*: inference of population structure from Multilocus sequence typing data. *Frontier in Microbiology*, 7, 1599.
- Quitoco, I.M.Z., Ramundo, M.S., Silva-Carvalho, M.C., Souza, R.R., Beltrame, C.O., de Oliveira, T.F. et al. (2013) First report in South America of companion animal colonisation by the USA1100 clone of community-acquired methicillin-resistant *Staphylococcus aureus* (ST30) and by the European clone of methicillin-resistant *Staphylococcus pseudintermedius* (ST71). *BMC Research Notes*, 6, 336.
- Rahman, M.M., Amin, K.B., Rahman, S.M.M., Khair, A., Rahman, M., Hossain, A. et al. (2018) Investigation of methicillin-resistant *Staphylococcus aureus* among clinical isolates from humans and animals by culture methods and multiplex PCR. *BMC Veterinary Research*, 14, 300.
- Roberts, M.C., Joshi, P.R., Greninger, A.L., Melendez, D., Paudel, S., Acharya, M. et al. (2018) The human clone ST22 SCCmec IV methicillin-resistant *Staphylococcus aureus* isolated from swine herds and wild primates in Nepal: is man the common source? *FEMS Microbiology Ecology*, 94, fty052.
- Rubin, J.E. & Chirino-Trejo, M. (2011) Prevalence, sites of colonisation, and antimicrobial resistance among *Staphylococcus pseudintermedius* isolated from healthy dogs in Saskatoon, Canada. *Journal of Veterinary Diagnostic Investigation*, 23, 351–354. <https://doi.org/10.1177/104063871102300227>
- Ruiz-Ripa, L., Simón, C., Ceballos, S., Ortega, C., Zarazaga, M., Torres, C. et al. (2021) *S. Pseudintermedius* and *S. aureus* lineages with transmission ability circulate as causative agents of infections in pets for years. *BMC Veterinary Research*, 17(1), 42. <https://doi.org/10.1186/s12917-020-02726-4>
- Rynhoud, H., Forde, B.M., Beatson, S.A., Abraham, S., Meler, E., Soares Magalhães, R.J. et al. (2021) Molecular epidemiology of clinical and colonising methicillin-resistant *Staphylococcus* isolates in companion animals. *Frontiers in Veterinary Science*, 8, 620491.
- Sasaki, T., Tsubakishita, S., Tanaka, Y., Ohtsuka, M., Hongo, I., Fukata, T. et al. (2012) Population genetic structures of *Staphylococcus aureus* isolates from cats and dogs in Japan. *Journal Clinical Microbiology*, 50, 2152–2155. <https://doi.org/10.1128/JCM.06739-11>
- Schmidt, V.M., Williams, N.J., Pinchbeck, G., Corless, C.E., Shaw, S., McEwan, N. et al. (2014) Antimicrobial resistance and characterisation of staphylococci isolated from healthy Labrador retrievers in the United Kingdom. *BMC Veterinary Research*, 10, 17.
- Sekhar, M., Rao, T. & Sharif, N. (2017) Nasal colonisation of methicillin resistant *Staphylococcus aureus* (MRSA) among dogs and dog handlers in Andhra Pradesh, India. *The Pharma Innovation*, 6, 86–90.
- Shallcross, L.J., Fragaszy, E., Johnson, A.M. & Hayward, A.C. (2013) The role of the Panton-valentine leucocidin toxin in staphylococcal disease: a systematic review and meta-analysis. *Lancet Infectious Diseases*, 13, 43–54. [https://doi.org/10.1016/S1473-3099\(12\)70238-4](https://doi.org/10.1016/S1473-3099(12)70238-4)
- Silva, V., Sousa, T., Gómez, P., Sabença, C., Vieira-Pinto, M., Capita, R. et al. (2020) Livestock-associated methicillin-resistant *Staphylococcus aureus* (MRSA) in purulent subcutaneous lesions of farm rabbits. *Foods*, 9, 439.
- Singh, A., Walker, M., Rousseau, J. & Weese, J.S. (2013) Characterisation of the biofilm-forming ability of *Staphylococcus pseudintermedius* from dogs. *BMC Veterinary Research*, 9, 93.
- Sleiniute, J. & Siugzdaite, J. (2015) Distribution of coagulase-positive staphylococci in humans and dogs. *Acta Veterinaria*, 84, 313–320.
- Somayaji, R., Priyantha, M.A., Rubin, J.E. & Church, D. (2016) Human infections due to *Staphylococcus pseudintermedius*, an emerging zoonosis of canine origin: report of 24 cases. *Diagnostic Microbiology and Infectious Disease*, 85, 471–476.
- Sudo, T., Terai, Y., Saegusa, S., Tsubakishita, S., Sasaki, T. & Hiramatsu, K. (2011) Epidemiological study of methicillin-resistant *Staphylococcus pseudintermedius* (MRSP) in healthy pet dogs in Japan. *The Japanese Journal of Veterinary Dermatology*, 17, 79–83.
- Valiakos, G., Pavlidou, E., Zafeiridis, C., Tsokana, C.N. & Del Rio Vilas, V.J. (2020) Antimicrobial practices among small animal veterinarians in Greece: a survey. *One Health Outlook*, 2, 7. <https://doi.org/10.1186/s42522-020-00013-8>
- Van Balen, J.C., Landers, T., Nutt, E., Dent, A. & Hoet, A.E. (2017) Molecular epidemiological analysis to assess the influence of pet-ownership in the biodiversity of *Staphylococcus aureus* and MRSA in dog- and non-dog-owning healthy households. *Epidemiology and Infection*, 145, 1135–1147.
- Wachtmeister, L. (2018) Antibiotic resistance in *Staphylococcus aureus* and *Staphylococcus pseudintermedius* isolated from milk, cattle and dogs in and around Kampala, Uganda, Volume 63, 39. Available from: https://stud.epsilon.slu.se/13667/7/wachtmeister_1_180912.pdf [Accessed 20th July 2021].
- Wan, M.T., Fu, S.Y., Lo, Y.P., Huang, T.M., Cheng, M.M. & Chou, C.C. (2012) Heterogeneity and phylogenetic relationships of community-associated methicillin-sensitive/resistant *Staphylococcus aureus* isolates in healthy dogs, cats and their owners: genetics of *Staph. aureus* in pets and owners. *Journal of Applied Microbiology*, 112, 205–213.
- Wedley, A.L., Dawson, S., Maddox, T.W., Coyne, K.P., Pinchbeck, G.L., Clegg, P. et al. (2014) Carriage of *Staphylococcus* species

in the veterinary visiting dog population in mainland UK: molecular characterisation of resistance and virulence. *Veterinary Microbiology*, 170, 81–88.

World Health Organization. (2017) Critically important antimicrobials for human medicine, 5th revision. Available from: <https://apps.who.int/iris/bitstream/handle/10665/255027/9789241512220-eng.pdf> [Accessed 3rd July 2022].

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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