The use of whole genome sequencing for the analysis of isolates belonging to the bacterial genus *Salmonella*



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Abstract

The global burden of disease from *Salmonella* infections is substantial and the increase of trade and travel across borders presented very real challenges, such as the investigation of multi-country outbreaks. The primary aim of this thesis was to examine WGS for the analysis of *Salmonella*, especially in regard to the public health applications of sequencing. A review was conducted in Chapter Two to establish the impact of whole genome sequencing on public health to date.

The analyses undertaken here were primarily conducted by upscaling the MLST-approach. In Chapter Three cgMLST was shown to be highly congruent with SNP-based approaches for outbreak investigations. The use of cgMLST enabled easier communication across borders as it was reference free and readily available online.

In Chapter Four the current core scheme was shown to be problematic for whole genus analyses. A new scheme was therefore developed and used for the identification and analysis of isolates from across the genus. This included the identification of novel subspecies and the reclassification of subspecies IIIa as a separate species – *S. arizonae*, as demonstrated in Chapter Five. This in turn enabled more accurate reporting of the salmonellae.

WGS can also be used to characterise datasets of related organisms as demonstrated through an analysis of serovar Enteritidis isolates from New South Wales, as shown in Chapter Six. This analysis identified differences between regions and countries in serovar Enteritidis strains and their AMR profiles.

This work provided an overview of the utility of WGS for public health purposes and expanded the current understanding of the molecular epidemiology of *Salmonella*.

Declaration

This thesis would not have been possible without the help of many people. Individuals and laboratories that contributed *Salmonella* sequences to either Enterobase or PubMLST improved or made possible many of the analyses conducted here. Furthermore, those individuals that developed freely available tools for the analysis of sequences were also highly instrumental.

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Abbreviations, Acronyms and Symbols

%	percent
°C	degrees Celsius
µm	micrometre
16S	16 Svedberg units
AMR	antimicrobial resistance
ANI	average nucleotide identity
$BIGS_{DB}$	bacterial isolate genome sequence database
cgMLST	core genome multilocus sequence typing
cgST	core genome sequence type
CRISPR	clustered regularly interspaced short palindromic repeats
DALY	disability adjusted life year
DDH	DNA-DNA hybridisation
DNA	deoxyribonucleic acid
eBG	eBurst group
EDR	extremely drug resistant
EU	European Union
H	flagella (antigen)
ITOL	interactive tree of life
km	kilometre
MCMC	Markov chain Monte Carlo
MDR	multidrug resistant
ML	maximum likelihood
MLEE	multilocus enzyme electrophoresis
MLST	multilocus sequence typing
MLVA	multiple-locus variable-number of tandem-repeats analysis
MVLST	multi-virulence-locus sequence typing
NCTC	national collection of type cultures
NJTree	neighbour-joining tree

NSW	New South Wales (Australia)
O	somatic (antigen)
OrthoANI	orthologous ANI
PCR	polymerase chain reaction
PFGE	pulsed-field gel electrophoresis
PHE	Public Health England
PT	phage type
rMLST	ribosomal multilocus sequence typing
rRNA	ribosomal ribonucleic acid
rST	ribosomal sequence type
SISTR	*Salmonella in silico* typing resource
SNP	single nucleotide polymorphism
SNV	single nucleotide variants
SPI	*Salmonella* pathogenicity island
SRA	short read archive
ST	sequence type
UK	United Kingdom
USA	United States of America
VNTR	variable-number tandem repeat
wgMLST	whole genome multi locus sequence typing
WGS	whole genome sequencing
WHO	World Health Organisation

Chapter One

Introduction

1.1 *Salmonella*

The salmonellae are flagellated rod shaped (Yousef and Carlstrom, 2003) gram-negative gammaproteobacteria that belong to the family Enterobacteriaceae (Ewing, 1986). The genus was named after D. E. Salmon (Miliotis and Bier, 2003), who was one of the first individuals to identify and characterise the bacteria from this genus. They are non-spore forming facultative anaerobes (Miliotis and Bier, 2003), with a length of 2 – 5µm and a width of 0.7 – 1.5µm (Yousef and Carlstrom, 2003; Pui *et al.*, 2011). Typically these bacteria are motile (Miliotis and Bier, 2003), with the exception of subspecies I serovars Gallinarum and its biovar Pullorum (Grimont and Weill, 2007).. These bacteria are non-fastidious and grow in temperatures from 5 – 47°C with an ideal temperature of 35 – 37°C (Guthrie, 1992) and pH between 4 – 9 with the optimum between 6.5 – 7.5 (Guthrie, 1992). Most of the salmonellae ferment lactose and produce sulphites, can hydrolyse urea and are able to grow on citrate as a sole carbon source (Jensen and Hoorfar, 2000; Annous and Gurtler, 2012)

1.2 Taxonomy and nomenclature of *Salmonella*

Salmonella represents a distinct genus of the family Enterobacteriaceae (Fitts *et al.*, 1983), as was confirmed through DDH (Crosa *et al.*, 1973), which has been regarded as the ‘gold-standard’ in genotypic species identification (Richter and Rosselló-Móra,

2009). In 2005 a judicial opinion (Prokaryotes, 2005) and accompanying commentary by Tindal et al. (Tindall *et al.*, 2005) split the genus into two species. These were *Salmonella bongori* (*S. bongori*) (Reeves *et al.*, 1989; Prokaryotes, 2005) and *Salmonella enterica* (*S. enterica*) (Prokaryotes, 2005), based on differences in their 16S rRNA sequence (Eng *et al.*, 2015). *S. enterica* was further comprised of six subspecies (Tindall *et al.*, 2005), based on differences in phenotypic traits (Grimont and Weill, 2007): *S. enterica* subspecies I (*enterica*), *S. enterica* subspecies II (*salamae*), *S. enterica* subspecies IIIa (*arizonae*), *S. enterica* subspecies IIIb (*diarizonae*), *S. enterica* subspecies IV (*houtenae*) and *S. enterica* subspecies VI (*indica*) (Tindall *et al.*, 2005) (Figure 1.1). The phenotypic distinctions among the subspecies have been further confirmed by DNA analyses, such as DDH and MLEE (Reeves *et al.*, 1989; Boyd *et al.*, 1996) and genetic characteristic analyses (Boyd *et al.*, 1996; McQuiston *et al.*, 2008).

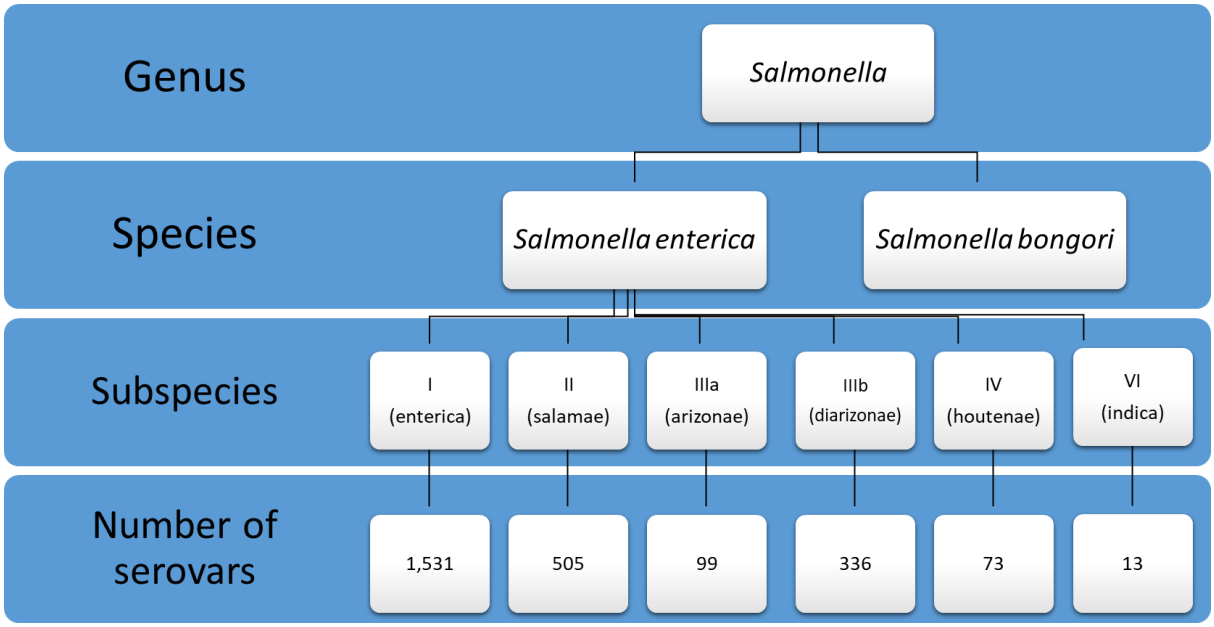


Figure 1.1: A breakdown of the *Salmonella* genus. *Salmonella* is composed of two species (*S. enterica* and *S. bongori*). The structure within the genus is then complicated by the presence of six subspecies in *S. enterica* and these subspecies all contain multiple serovars. The number of serovars per subspecies varies greatly. The number of serovars was taken from the latest Kauffmann-White scheme and will therefore be slightly outdated as new serovars are identified relatively frequently.

Novel subspecies of *S. enterica* have also been proposed, such as subspecies VII (Boyd *et al.*, 1996), which was identified initially through MLEE (Boyd *et al.*, 1996) and was confirmed as a distinct cluster using genetic approaches (McQuiston *et al.*, 2008). A core genome SNPs analysis also identified a further three potential novel subspecies (novel subspecies A, B and C) (Alikhan *et al.*, 2018). These subspecies, however, have yet to be formally recognised by the judicial committee.

Salmonella can be further subdivided into serovars (or serotypes) based on somatic, capsular and flagellar antigenic determinants (Brenner *et al.*, 2000). To date over 2,500 serovars of *Salmonella* have been officially recognised (Grimont and Weill, 2007), of which over 1,500 belong to subspecies I (Grimont and Weill, 2007) and the remaining serovars are split between *S. bongori* and *S. enterica* subspecies II, IIIa, IIb, IV and VI (Grimont and Weill, 2007). The majority of *Salmonella* serovars were named after the location at which the strain was first isolated and characterised, although a small percentage of serovars are named after individuals, food sources or are compositions of the symptom and host (Gossner *et al.*, 2016).

1.3 Global burden of *Salmonella*

Salmonella has been responsible for the greatest burden of all foodborne diseases, in terms of years of life lost and years lost due to disability (Kirk *et al.*, 2015). When the burdens from all *Salmonella* infections were combined an estimated loss of 8.76 million DALYs per year was given (Kirk *et al.*, 2015). When combined non-typhoidal *Salmonella* infections (diarrhoeal and invasive) were responsible for an estimated loss of 4.07 million DALYs (Kirk *et al.*, 2015), therefore Typhi and Paratyphi A infections were responsible for the loss of 4.69 million DALYs per year (Kirk *et al.*, 2015).

Of all foodborne pathogens *Salmonella* was the organism most reported to have contributed to the death of an individual within the USA (Barton Behravesh *et al.*, 2011). It was estimated that the *Salmonella* species were responsible for 93.8 million cases of gastroenteritis globally and 155,000 deaths each year (Majowicz *et al.*, 2010). An estimated further 3.4 million cases of infection and 681,316 deaths were caused

by invasive nontyphoidal *Salmonella* infections (Ao *et al.*, 2015). Infection with *Salmonella* Typhi leading to Typhoid fever was responsible for an estimated 21,650,974 illnesses and 216,510 deaths in 2000 (Crump, Luby and Mintz, 2004) and paratyphoid fever was estimated to have caused 5,412,744 illnesses (Crump, Luby and Mintz, 2004).

S. enterica was responsible for the majority of *Salmonella* infections. Fifty serovars, all of which belong to subspecies I, were responsible for 99% of cases in humans and domestic mammals (CDC, 2008). *S. enterica* serovar Enteriditis was the largest single cause of Salmonella infection globally, accounting for between 40 - 60% of human cases (Galanis *et al.*, 2006; Hendriksen *et al.*, 2011) and many foodborne disease outbreaks (Inns *et al.*, 2015; Pärn *et al.*, 2017; Kanagarajah *et al.*, 2018). The next most common serovars were Typhimurium and Newport, which were responsible for 12% and 4% of cases respectively (Galanis *et al.*, 2006). Serovar Enteritidis was particularly prevalent in Africa, Europe, North America, and parts of Asia (Galanis *et al.*, 2006; Centers for Disease Control and Prevention (CDC), 2016).

While non-subspecies I *Salmonella* were found in the environment and within products for human consumption, human disease caused by these serovars has been rare (Boore *et al.*, 2015). This is because non-subspecies I *Salmonella* are only opportunistic pathogens of humans (Lamas *et al.*, 2018), with the majority of human cases having affected vulnerable individuals (Nair *et al.*, 2014; Y.-C. Lee *et al.*, 2016). These infections have, however, caused complications (Mukai, Agatsuma and Ideura, 2018) and deaths (Mahajan *et al.*, 2003) in some circumstances.

1.4 Sources of *Salmonella* infection

The salmonellae have been found in many different hosts (Lamas *et al.*, 2018), including mammals (Flockhart *et al.*, 2017), birds (Mellor *et al.*, 2010), reptiles (Whiley, Gardner and Ross, 2017), fish (Nguyen *et al.*, 2016) and crustaceans (Nguyen *et al.*, 2016). *S. enterica* subspecies I has primarily been isolated from warm-blooded animals, while non-subspecies I *Salmonella* were most commonly associated with cold-blooded animals (Lamas *et al.*, 2018). All of the *S. enterica* subspecies and *S. bongori* have, however, been isolated from both warm (Zottola *et al.*, 2013) and cold-blooded animals (Geue and Löschner, 2002).

S. enterica subspecies I was often associated with chickens and eggs, with over 16 serovars being isolated from these sources (Roy *et al.*, 2002) but other reservoirs such as cattle and pigs have also been documented (Shekhar and Singh, 2015). Serovars have also been isolated from sources including water, soil, feed, organic fertilisers, produce, wildlife and sewage, with outbreaks from produce and water rising (Haley, Cole and Lipp, 2009; Gorski *et al.*, 2011; Hoszowski *et al.*, 2012). Once an environment has been infected, *Salmonella* can persist for long periods of time (Rodriguez *et al.*, 2006) and its presence within animal feeds or ingredients has been previously demonstrated (Maciorowski *et al.*, 2004; Rodriguez *et al.*, 2006; Alali *et al.*, 2010). The majority of subspecies I infections have been linked to food products (Hoelzer, Moreno Switt and Wiedmann, 2011), many of which have been associated with the consumption of meat; however other food products have also been implicated, including fruits, nuts and vegetables (Andino and Hanning, 2015).

Reptiles are thought to be a natural reservoir for non-subspecies I (Schröter *et al.*, 2004; Nowakiewicz *et al.*, 2012) and its estimated that more than 1% of households in the USA and Europe are now home to either a reptile or amphibian species (American Veterinary Medical Association, 2007; Romero *et al.*, 2016). A study examining 16 pet snakes found 13 of them were infected with subspecies IIIb (Schröter *et al.*, 2004) and another study identified subspecies II isolates in 8 out of 80 pet turtles, most of which were infected with more than one strain (Nowakiewicz *et al.*, 2012). As well as reptilian pets, (Whiley, Gardner and Ross, 2017) non-subspecies I has been isolated from reptile meat for consumption (Magnino *et al.*, 2009) and some 'traditional medicines' (Kraus, Guerra-Bautista and Alarcón-Segovia, 1991). Non-subspecies I isolates have been identified in products for human consumption, including poultry (Mellor *et al.*, 2010), cattle (Rodriguez *et al.*, 2006), sheep (Sörén *et al.*, 2015), pork (Rodriguez *et al.*, 2006) and fresh produce (Rodriguez *et al.*, 2006), as well as being found in wild animals (Millan *et al.*, 2004; Zottola *et al.*, 2013).

1.5 *Salmonella* pathogenicity

Salmonella are facultative intracellular pathogens (Jantsch, Chikkaballi and Hensel, 2011) and almost all *Salmonella* are pathogenic, as they can invade, replicate and survive in host cells, resulting in disease (Andino and Hanning, 2015). Genes on SPI-1 enabled the invasion into non-phagocytic host cells and genes from SPI-2 enabled the survival and replication of *Salmonella* in a host cell (Haraga, Ohlson and Miller, 2008). Host cells can be invaded via either bacteria-mediated invasion or by phagocytosis (Jantsch, Chikkaballi and Hensel, 2011). Survival and replication within the host cell is enabled through the creation of a membrane-bound compartment

(Szeto *et al.*, 2009). Once inside the host cell *Salmonella* inject effector proteins across the membrane and into the host cytoplasm, which alter host cell endosomal trafficking and contribute to bacterial replication (Kuhle and Hensel, 2004). These effector proteins also help with exclusion or evasion of anti-microbial compounds produced by the host cell (Jantsch, Chikkaballi and Hensel, 2011).

1.6 Symptoms and complications of *Salmonella* infections

Salmonella infections can result in gastroenteritis, invasive gastroenteritis, typhoid fever and septicaemia (Cherubin *et al.*, 1969). The majority of *Salmonella* infections result in gastroenteritis, which includes symptoms such as: non-bloody diarrhoea, vomiting, nausea, abdominal cramps, general pains and headaches (Acheson and Hohmann, 2001; Eng *et al.*, 2015). Infection normally occurs 6 – 72 hours following exposure and is generally self-limiting and will normally have cleared in 4 – 7 days (Cash-Goldwasser and Barry, 2018). Approximately 5% of people develop bacteraemia or a focal infection (such as meningitis or osteomyelitis) following an infection with *Salmonella* (Cash-Goldwasser and Barry, 2018).

Bacteraemia occurs when the bacteria enters the bloodstream after intenstinal invasion. The serovars Dublin and Cholearaesuis are highly associated with the developments of bacteraemia (Cash-Goldwasser and Barry, 2018). Rates of invasive infections are often higher among infants, the elderly and the immunocompromised (Cash-Goldwasser and Barry, 2018). High fever is a characteristic symptom of bacteraemia (Eng *et al.*, 2015) and the immune response can lead to septic shock that

has a high mortality rate (Ryu *et al.*, 1995; Arii *et al.*, 2002; Cash-Goldwasser and Barry, 2018).

Typhoid and paratyphoid fevers (caused by serovars Typhi and Paratyphi A, B and C) (Eng *et al.*, 2015) normally present6 – 30 days post infection but initial symptoms can be non-specific such as, diarrhoea and vomiting or respiratory symptoms (Sinha *et al.*, 1999; Lin *et al.*, 2000). Symptoms often include increasing fatigue and an increasing fever that can rise to 38°C–40°C by the third or fourth day of illness (Cash-Goldwasser and Barry, 2018). About 10 – 15% of patients can go on to develop severe disease (Bhan, Bahl and Bhatnagar, 2005) and complications include gastrointestinal bleeding, intestinal perforation and encephalopathy (Parry *et al.*, 2002; World Health Organisation. Department of Vaccine and Biological, 2003). Serious complications generally occur 2–3 weeks after the onset of illness and can include life-threatening intestinal haemorrhage or perforation (Cash-Goldwasser and Barry, 2018). Intestinal perforation is predicted to occur in 1 – 3% of cases and the ileum was identified as the most common site for perforation (van Basten and Stockenbrügger, 1994). Left untreated the disease can persist for a month (Cash-Goldwasser and Barry, 2018).

Further to this sequalae include but are not limited to: Reiter's Syndrome, reactive arthritis, haemolytic anaemia, irritable bowel syndrome, Crohn's disease, ulcerative colitis, cellulitis, urinary tract infections, pneumonia, endocarditis and meningitis and Guillain-Barré Syndrome (Arii *et al.*, 2002; Helms, Simonsen and Mølbak, 2006).

1.7 Laboratory Diagnosis of *Salmonella*

Microbiologically, bacterial species and subspecies have been identified through morphological and biochemical traits (Parker, Tindall and Garrity, 2015). For the identification of serovars the Kauffmann-White scheme (Grimont and Weill, 2007) was developed, it used O and H antigens to identify an isolate (Brenner *et al.*, 2000). Initially the O antigens, which are polysaccharides found specifically in the lipopolysaccharide coat, are used to provide a broad group to an isolate (Grimont and Weill, 2007). The H antigens are then used to fully identify the serovar by providing a second grouping for an isolate, there are five complexes the antigens fall into: E, G, L, Z_4 and 1 (Grimont and Weill, 2007). These antigens are either expressed monophasically or diphasically (with the notable exception of Gallinarum which does not express flagella antigens) (Grimont and Weill, 2007). Instead of performing full serotyping using the Kauffmann-White scheme many clinical laboratories have performed agglutination reactions specific to antibodies of the O antigens, which provides enough specificity to identify that an infection is caused by *Salmonella* (Wattiau *et al.*, 2008).

However serotyping has multiple issues, one of the largest of which is that it cannot always identify genetically distinct lineages (Sangal *et al.*, 2010; Achtman *et al.*, 2012). Serotyping can be expensive due to the need for well-trained technicians (Herrera-León *et al.*, 2007; Achtman *et al.*, 2012) and time consuming, if an isolate requires additional work to enhance expression of antigens (APHL, 2014). Approximately 10% of isolates can become impossible to type due to problems with autoagglutination or a lack of expressed surface antigen (Wattiau *et al.*, 2008).

MLEE was capable of identifying lineages, that corresponded to serovars (Achtman *et al.*, 2012) by staining and running enzymes on an electrophoretic gel (Achtman *et al.*, 2012) and comparisons in enzyme mobility created a specific score for a serovar. MLEE was therefore used briefly for the identification of serovars (Boyd *et al.*, 1993; Brenner *et al.*, 2000); however the need for potentially hundreds of gels to score a range of isolates (Selander *et al.*, 1986) was considerably problematic. This, coupled with some serovars being composed of multiple genetically unrelated lineages, meant that MLEE was never widely accepted (Achtman *et al.*, 2012).

The longest standing genetic approach has been MLST (Maiden *et al.*, 1998). MLST combined alleles from serval conserved housekeeping genes from across the genome to create a single profile for an isolate (Maiden *et al.*, 1998). The use of multiple genes and their distribution around the genome made MLST more reliable by protecting against horizontal gene transfer (Jolley, Bliss, *et al.*, 2012). MLST has proven to predict the serovar of an isolate with a high degree of accuracy (Ranieri *et al.*, 2013) and unlike other methods, such as MLEE, it was easily comparable between laboratories (Maiden *et al.*, 1998). The most significant drawback to MLST was that it could not do fine typing of monomorphic or highly homogenous serovars and could therefore not be used in outbreak analyses (Urwin and Maiden, 2003).

Multiplex PCR was also suggested for the rapid identification of serovars (Akiba, Kusumoto and Iwata, 2011; Li *et al.*, 2014), as MLST was often too slow (Achtman *et al.*, 2012). Multiplex PCR was found to be quick, relatively cheap and effective for the identification of common serovars (Levy *et al.*, 2008; Akiba, Kusumoto and Iwata,

2011; Li *et al.*, 2014) but could not be used for the identification of all serovars (Levy *et al.*, 2008; Akiba, Kusumoto and Iwata, 2011; Li *et al.*, 2014).

Some reference laboratories have adopted WGS for the routine identification and surveillance of *Salmonella* (Ashton *et al.*, 2016). This has therefore replaced conventional serotyping (Ashton *et al.*, 2016) with sequence based approaches such as MLST (Maiden *et al.*, 1998) or the genomic identification of antigens using tools such as Seqsero (Zhang *et al.*, 2015) and SISTR (Yoshida *et al.*, 2016).

1.8 Monitoring *Salmonella*

The Kauffmannn-White scheme, facilitated international communication and comparison due to annual updates and maintenance by the WHO coordinated reference laboratory, located at the Insitut Pasteur (Paris, France) (Grimont and Weill, 2007) but lacked the resolution necessary for outbreak detection and characterisation. MLST was also incapable of fine typing and therefore could not be solely used for outbreak analyses of the common serovars either (Urwin and Maiden, 2003).

Phage typing has been used for a considerable amount of time in the epidemiological characterisation of common *Salmonella* serovars (Baggesen *et al.*, 2010) for which schemes have been developed, such as Typhimurium and Enteritidis (Rabsch, 2007). The PTs within a serovar are determined via the pattern of susceptibility to lysis by a set of phages with different specificities, with each unique strain having their own phage type (Rabsch, 2007). The increased discriminatory power of phage typing

enabled the characterisation of serovars into specific strains that can then be used in source attribution and outbreak investigations (Baggesen and Wegener, 1994; Hald, Lo Fo Wong and Aarestrup, 2007). Phage typing is, however, difficult to conduct and relies on experienced technicians and well maintained reference systems for the production of accurate results (Baggesen *et al.*, 2010). Phage typing is not always accurate as outbreaks can also contain multiple PTs (Inns *et al.*, 2017). For example had conventional PT surveillance been employed in one outbreak approximately 30% of isolates would have been lost from the outbreak definition (Inns *et al.*, 2017).

MLVA has also been used for the subtyping of *Salmonella* serovars and outbreak communications (Nadon *et al.*, 2013; Inns *et al.*, 2015). MLVA determined the number of tandem repeats at multiple VNTR loci within a genome, which are caused by replication errors (Lindstedt, 2005; Nadon *et al.*, 2013). The alleles from the loci analysed then formed the MLVA profile for the strain of interest (Nadon *et al.*, 2013). Each unique allelic profile for each locus was assigned a number to enable the easy communication of profiles (Lindstedt *et al.*, 2004). As with phage typing MLVA schemes have not been established for all serovars (Nadon *et al.*, 2013) and MLVA can lack the fine resolution needed to fully characterise an outbreak (Octavia *et al.*, 2015). For example, an outbreak of Typhimurium caused by multiple strains indicated that the source had been contaminated with multiple strains (Octavia *et al.*, 2015); however, this was not observed when using MLVA, as all isolates shared the same profile (Octavia *et al.*, 2015).

PFGE fingerprinting also provided increased resolution in outbreak analyses (Gerner-Smidt *et al.*, 2006) and was used for the surveillance of *Salmonella* across countries and borders (Gatto *et al.*, 2006). PFGE is a gel-based approach that enabled characterisation of larger DNA molecules (Herschleb, Ananiev and Schwartz, 2007). The direction of electrical field is periodically changed which required molecules to change their orientation to maintain motion through the gel (Herschleb, Ananiev and Schwartz, 2007). These movements through the gel created a pattern that could be used for the identification of pathogen strains (Swaminathan *et al.*, 2001) and large databases were established with the development of PulseNet in order to facilitate communication (Swaminathan *et al.*, 2001, 2006). PFGE has been utilised very effectively for the identification and communication of *Salmonella* outbreaks (Sandt *et al.*, 2006) and has enabled the tracking of outbreaks (Sandt *et al.*, 2006). However, PFGE profiles were difficult to compare among laboratories (Harbottle *et al.*, 2006), as they required highly standardised approaches (Swaminathan *et al.*, 2001) and a global PFGE database proved too complex and costly to implement (Nadon *et al.*, 2017). With the increasing uptake of WGS by laboratories (Ashton *et al.*, 2016) for the routine surveillance and tracking of foodborne outbreaks (Inns *et al.*, 2015, 2017; Kanagarajah *et al.*, 2018), PulseNet International has identified cgMLST as the surveillance system to replace PFGE (Nadon *et al.*, 2017).

Chapter Two

Review: The increasing utility of whole genome sequencing for *Salmonella* investigations in a public health setting

Abstract

WGS has become increasingly used for the analysis of *Salmonella* isolates and could have a considerable impact on public health. This review looks at the increasing utility of WGS for the analysis of *Salmonella*¸ including the identification of *Salmonella* serovars, the detection of clusters and outbreaks, novel approaches to outbreaks identification, further investigation of outbreaks and the analysis of virulence genes and AMR profiles within isolates. The results demonstrated the impact of WGS on the detection and identification of *Salmonella* isolates, outbreak investigations and the characterisation of *Salmonella* isolates. The studies described here demonstrated the uses of WGS for providing increased resolution in outbreaks and for increasing the certainty with which outbreak sources can be identified. WGS was of particular utility when used for the analysis of isolates from across multiple countries. These analyses were all performed using at least some WGS and many of these analyses would not have been possible or would have been considerably more challenging without the use of WGS. The range of uses for WGS shown here demonstrates the utility of WGS as a 'one-stop' shop for the analysis of *Salmonella.*

2.1 Introduction

Over the past decade the use of WGS has increased dramatically (Revez *et al.*, 2017) and this is reflected within the literature. Searches of the web of science literature database revealed an upward trend in the number of publications that used WGS for the analysis of *Salmonella* isolates that was greater than the general increase in papers published per year (Figure 2.1).

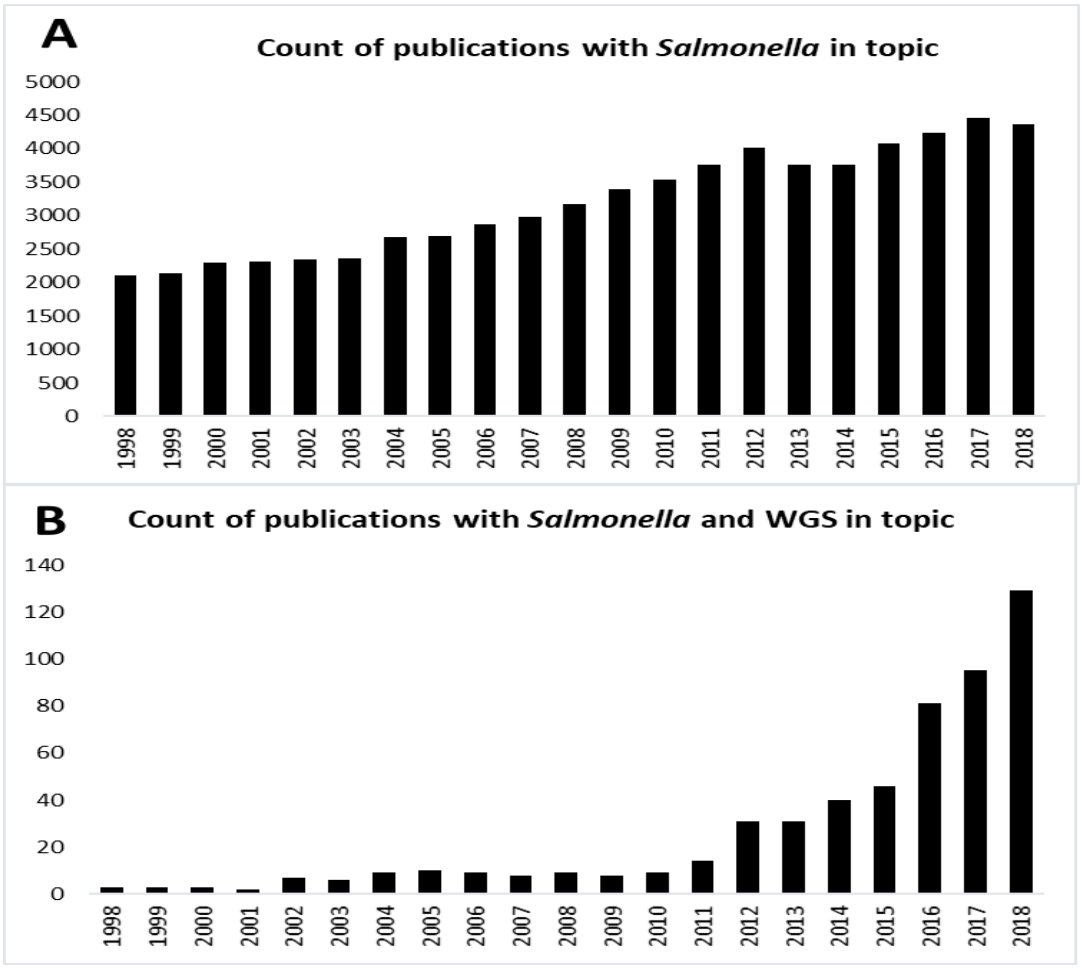


Figure 2.1: Graphs showing the number of papers published with *Salmonella* and *Salmonella* and WGS within the topic in the web of science literature database. Both graphs revealed a general upward trend in the number of publications published per year.

1a: The number of papers that had *Salmonella* in the topic that were available in the web of science database. Over the last twenty years there had been a general upward increase in the number of papers published with *Salmonella* in their topic. The increase in the number of papers did, however, appear to slow after 2012.

1b: The number of papers that had *Salmonella* and 'whole genome sequencing' within the topic of the paper that were available in the web of science database. There was a considerable increase in the number of papers that contained whole genome sequencing, particularly from 2008 to 2018.The increase in papers with whole genome sequencing within their topic was considerably greater than the increase in the number of papers published with *Salmonella* in their topic.

Analysis of WGS has made a considerable impact within a public health setting (Ashton *et al.*, 2016) and the roles performed by public health facilities (Figure 2.2). This is particularly true within the PHE reference laboratories, which have implemented WGS for routine surveillance of foodborne pathogens (Grant *et al.*, 2018). Since April 2014 all *Salmonella* isolates received by PHE have undergone WGS (Loman *et al.*, 2016) and since 2015 WGS has been used as a replacement for the majority of conventional serotyping (Ashton *et al.*, 2016). Since then WGS has been implemented or is being implemented globally for routine surveillance (Holmes *et al.*, 2018) or outbreak analysis (Leekitcharoenphon *et al.*, 2014) within Africa (Fashae, Leekitcharoenphon and Hendriksen, 2018), Asia (Yan *et al.*, 2015), Europe (ECDC, 2016; Revez *et al.*, 2017; Holmes *et al.*, 2018), Oceania (Ford *et al.*, 2018; Lindsay *et al.*, 2018) North America (den Bakker *et al.*, 2014; Angelo *et al.*, 2015) and South America (Toro *et al.*, 2016).

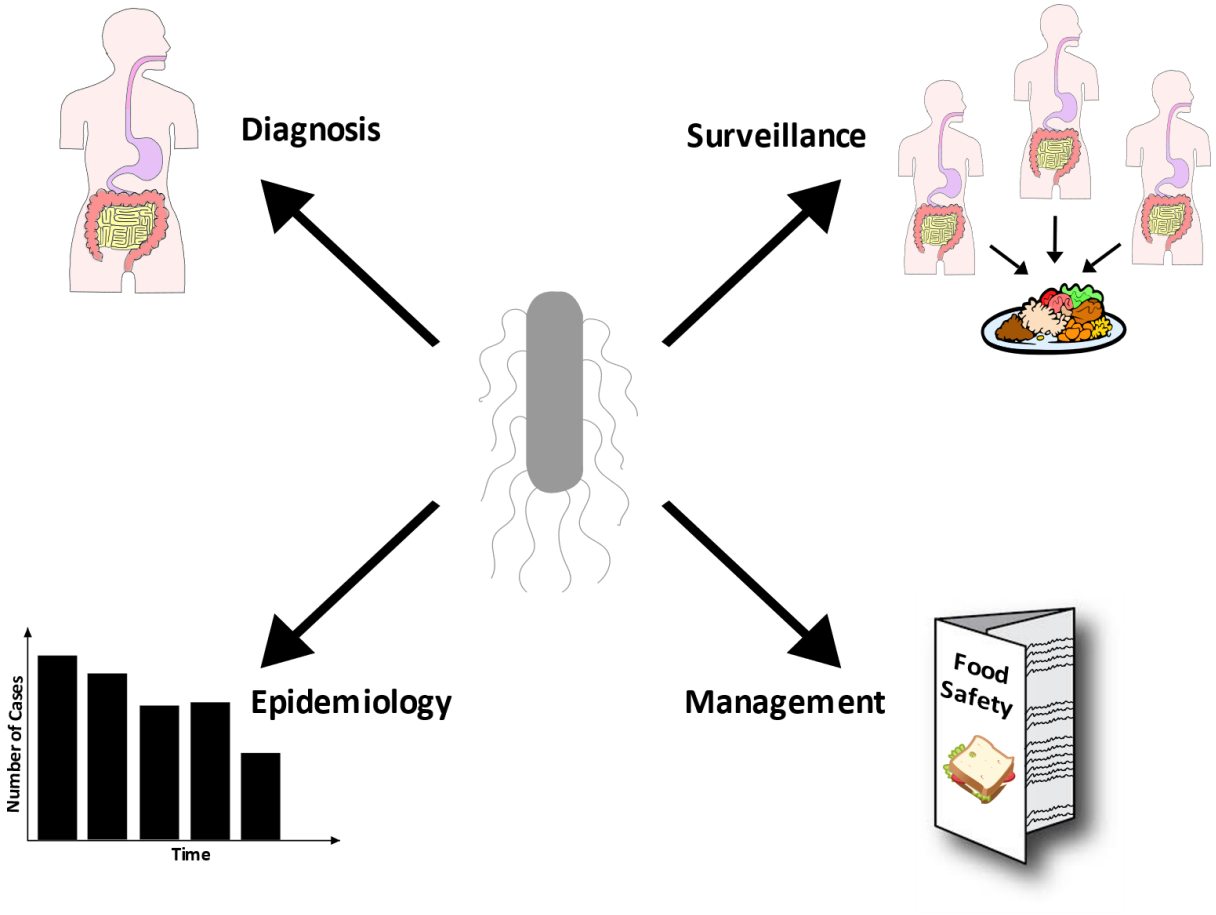


Figure 2.2: The four key roles played by public health laboratories in regard to gastrointerestinal infections. Diagnosis focuses on the routine identification of a pathogen, for instance from a clinical or food sample. Surveillance focuses on the detection and investigation of outbreaks. Epidemiology focuses on the general trends, for example if the number of cases of *Salmonella* has increased within a year. Management focuses on interventions, such as the production of operational guidelines and informative literature.

The replacement of conventional approaches with WGS for the analysis of pathogens, meant that isolates could be routinely identified and characterised using the genome sequence (Grant *et al.*, 2018). This enabled the identification of traits such as serovar, sequence type (ST), antimicrobial resistance (AMR) and virulence from the genotype, rather than relying on a panel of phenotypic tests in order to determine these properties

(Moran-Gilad, 2017). Biochemical approaches for identification and characterisation also require a wide range of microbiological expertise and are low throughput (Herrera-León *et al.*, 2004). Not only is WGS being implemented for outbreak analysis and routine surveillance (Angelo *et al.*, 2015; ECDC, 2016; Ford *et al.*, 2018) but the WGS-based cgMLST scheme is now also the primary focus of PulseNet for global investigations of major foodborne pathogens (Nadon *et al.*, 2017).

Salmonella is one of the pathogens that PulseNet aims to monitor and report globally (Swaminathan *et al.*, 2006). The salmonellae are gram-negative gammaproteobacteria belonging to the family Enterobacteriaceae (Ewing, 1986) and are comprised of two formally recognised species *Salmonella bongori (S. bongori)* (Reeves *et al.*, 1989; Prokaryotes, 2005) and *Salmonella enterica (S. enterica)* (Prokaryotes, 2005). *S. enterica* is divided into a further six formally recognised subspecies (Tindall *et al.*, 2005): *Salmonella enterica* subspecies I (*enterica),* *Salmonella enterica* subspecies II (*salamae*), *Salmonella enterica* subspecies IIIa (*arizonae)*, *Salmonella enterica* subspecies IIIb (*diarizonae)*, *Salmonella enterica* subspecies IV (*houtenae*) and *Salmonella enterica* subspecies VI (*indica*) (Tindall *et al.*, 2005). Finally these subspecies are divided into more than 2,500 serovars, the majority of which belong to subspecies I (Grimont and Weill, 2007). The *Salmonella* genus is estimated to be responsible for 80.3 million cases of foodborne gastroenteritis and 155,000 deaths annually (Majowicz *et al.*, 2010). Non-typhoidal *Salmonella* also have the highest burden of all foodborne infections, with an estimated 4.07 million DALYs lost each year (Kirk *et al.*, 2015).

Conventionally, *Salmonella* was typed using the Kauffmann-White scheme, which was based on the serological detection of O and H antigens (Grimont and Weill, 2007) but serotyping is not always an accurate reflection of the genetic relatedness of *S. enterica* serovars (Harbottle *et al.*, 2006; Sangal *et al.*, 2010). For example, serovar Newport is comprised of multiple genetically distinct lineages that all have the same O and H antigens (Sukhnanand *et al.*, 2005; Harbottle *et al.*, 2006; Sangal *et al.*, 2010). While serotyping aided in the detection and investigation of larger outbreaks by offering higher specificity than speciation (Olsen *et al.*, 2001), it was incapable of detecting smaller or more geographically diverse outbreaks (Bender *et al.*, 2001), as it lacked the required specificity (Tauxe, 2006). Increased resolution was gained through PFGE fingerprinting (Bender *et al.*, 2001), which made global communication possible through the PulseNet initiative (Swaminathan *et al.*, 2006). These data required highly standardised approaches (Swaminathan *et al.*, 2001), which made cross laboratory comparisons difficult (Harbottle *et al.*, 2006) and a global PFGE database was found to be too costly and complex to implement (Nadon *et al.*, 2017).

Reliable alternatives were found in nucleotide based typing schemes, such as MLST (Maiden *et al.*, 1998). These schemes were readily available internationally, as they were hosted on web-based servers (Maiden *et al.*, 1998) and the protocols for generating STs were easily replicated (Maiden *et al.*, 1998). The MLST approach proved to be scalable in both the number of isolates to be analysed and resolution (Maiden *et al.*, 2013) and were an accurate reflection of the genealogy of the species (Achtman *et al.*, 2012). The most significant problem for seven locus MLST was that it could not identify outbreaks caused by distinct but closely related bacteria (Baker *et al.*, 2008; Maiden *et al.*, 2013). High throughput sequencing technologies have made

WGS-based analyses increasingly affordable and practical, therefore allowing for high-resolution isolate characterisation (Bakker *et al.*, 2011; Inns *et al.*, 2015; Quick *et al.*, 2015; Dallman *et al.*, 2016). This has facilitated the adoption of WGS for routine surveillance and outbreak investigation (Ashton *et al.*, 2016; Nadon *et al.*, 2017) and in turn has seen the start of a new era within public health – the genomic era.

WGS can be used to identify *Salmonella* species, subspecies and serovars, as demonstrated within this thesis. This review aims to demonstrate the utility of WGS within investigations of *Salmonella* in public health settings. WGS analyses can impact isolate detection and classification, outbreak investigations and characterisation of the isolates, including analysis of virulence factors and AMR analysis. The sequencing of *Salmonella* genomes may enable a 'one-stop shop' approach to *Salmonella* identification, characterisation and investigation of isolates. An increased number of *Salmonella* outbreaks could be detected and fully chacterised from the inclusion and exclusion of isolates that fit the case definition to the confirmation of the source of the outbreak.

2.2 Detection and Identification of *Salmonella*

2.2.1 Identification of *Salmonella* isolates using WGS

A major concern with the adoption of WGS for routine identification of *Salmonella* isolates is that sequence-based typing may not be concordant with conventional serotyping (Ashton *et al.*, 2016; Yachison *et al.*, 2017). The loss of this information could hinder the maintenance of historical records, established communication systems and surveillance (Yachison *et al.*, 2017). The majority of isolates are identifiable through WGS based MLST, with more than 95% concordant with traditional methods (Ashton *et al.*, 2016). The most common cause of mismatches occurred when isolates belonging to two different serovars shared the same ST, such as Saintpaul and Haifa isolates which can both belong to ST49 (Ashton *et al.*, 2016). When this occurs it is possible to identify the serovar using WGS with online tools such as SISTR (Yoshida *et al.*, 2016) and SeqSero (Zhang *et al.*, 2015).

These approaches identify the serovar of an isolate from the genome sequence of its antigens (Zhang *et al.*, 2015; Yoshida *et al.*, 2016) and have demonstrated congruence with conventional serotyping and can also identify novel serovars (Yachison *et al.*, 2017; Robertson *et al.*, 2018). A high level of congruency has also been observed between conventional serotyping and MLST from WGS for the identification of novel serovars, with over 75% of serologically novel isolates also being identified as novel using MLST approaches (Bale *et al.*, 2016). A combinatorial approach to serovar identification using these tools will therefore enable maintenance of current systems (Yachison *et al.*, 2017), especially when coupled with datasets which have been validated using typing resources that are available online, to help

ensure accurate identification of isolates (Robertson *et al.*, 2018). A widespread adoption of WGS is likely to change how serotyping is viewed and while it is likely that the nomenclature will persist, it is also likely that the information encoded by serovar will decline in importance for the identification of novel serovars and for informing epidemiological investigations.

WGS was used to confirm the presence of *Salmonella* species from imported fresh leaves as part of routine surveillance performed by PHE (McLauchlin *et al.*, 2018). This analysis identified *Salmonella* from 44 samples, including curry leaves, betel and other leaf types (McLauchlin *et al.*, 2018). SNP analysis on 15 of the isolates found no groups within 50 SNPs, except for three serovar Newport isolates which were collected from a single retailer on the same day (McLauchlin *et al.*, 2018).

The use of WGS was also able to reveal a laboratory-acquired infection of serovar Typhimurium (Alexander *et al.*, 2016). The initial investigation concluded that the infection had not been acquired within the laboratory, as the PFGE profile of the infection isolate (Blnl) was different from the laboratory strain that was the prime infection candidate (Alexander *et al.*, 2016). WGS SNP analysis of all isolates that had identical PFGE patterns to the infection revealed that one of them had an identical SNP profile to the infection isolate and was therefore implicated as the source of infection (Alexander *et al.*, 2016). These results demonstrated the usefulness of WGS for distinguishing between highly related laboratory strains and detecting laboratory acquired infections (Alexander *et al.*, 2016). The identification of all laboratory acquired

infections is important as it can help to inform a laboratory's standards of practice, helping to prevent further infections from being acquired.

For serovars that do not occur in all countries, such as Typhi, a detailed knowledge of the global population gained from WGS-based typing can help to monitor the global spread of the disease and detect recent introductions into new locations or identify the source of infection (Wong, Baker, *et al.*, 2016). Increased knowledge of the origin of an infection can aid in prevention by focusing an investigation on specific sources. It can also aid in the treatment of isolates with bacterial resistance, for instance isolates from a specific source may share a consistent AMR profile.

2.2.2 Detection of *Salmonella* clusters and outbreaks

One of the most significant advantages of using WGS over biochemical techniques in public health is the ability to easily determine how closely related isolates are. SNP typing of WGS is more discriminatory than phage type (Ziebell *et al.*, 2017), PFGE (Deng *et al.*, 2015; Taylor *et al.*, 2015; Ziebell *et al.*, 2017), MLVA (Deng *et al.*, 2015; Ziebell *et al.*, 2017) and CRISPR-MVLST (Deng *et al.*, 2015). High concordance between techniques, such as CRISPR and WGS methods have been observed (Xie *et al.*, 2017), however WGS provided increased resolution over CRISPR (Xie *et al.*, 2017). Conversely phage typing has been demonstrated to be evolutionarily disjunct from WGS based phylogenies in both serovars Typhimurium (Zheng *et al.*, 2014) and Enteritidis (Pang *et al.*, 2012), suggesting that it may not be appropriate for inferring any phylogenetic relationships within the salmonellae (Pang *et al.*, 2012; Zheng *et al.*, 2014). Core genome analysis has also been shown to have higher resolution than 16S

rRNA sequencing and MLST (Leekitcharoenphon *et al.*, 2012). WGS also has a high correlation with epidemiological data (Deng *et al.*, 2015; Ziebell *et al.*, 2017).

The clustering of isolates into levels of relatedness can help to determine if incidences of infection are sporadic or if they are potentially from a common source. Using WGS identifies more clusters than conventional detection methods and many of these clusters can also be linked with statistical significance to a common epidemiological cause (Ford *et al.*, 2018; Mook *et al.*, 2018; Waldram *et al.*, 2018). Some caution is necessary when using SNP typing because while clustering is relatively stable (Usongo *et al.*, 2018), the use of different reference sequences and low coverage reads can alter SNP distances considerably (Saltykova *et al.*, 2018). The choice of reference and cut-offs for cluster detection should therefore be considered as they can vary across SNP systems and wherever possible the reference should belong to the same serovar as the isolates being analysed (Gymoese *et al.*, 2017; Saltykova *et al.*, 2018).

While analysis of WGS is superior to conventional clustering approaches, WGS alone cannot determine if strains are part of an outbreak (Leekitcharoenphon *et al.*, 2014). The identification of a cluster of isolates as an outbreak still relies on epidemiological investigation (Pightling *et al.*, 2018); however, when some of the clusters identified using WGS are coupled with epidemiological investigation they can be identified as outbreaks, which they previously wouldn't have been. Small clusters of isolates, including those that belong to a single MLVA clone (Phillips *et al.*, 2016), which were previously undetected using conventional approaches can be found when analysed

with WGS and investigations can provide epidemiological links between some of these clusters (Phillips *et al.*, 2016; Waldram *et al.*, 2018). Furthermore, 'slow-burn' outbreaks (Figure 2.3) can be detected using WGS. These outbreaks, especially of common serovars, can persist below the thresholds required to trigger an outbreak alert over significant periods of time. Routine analysis of WGS can identify these clusters and epidemiological investigation may determine a common exposure, therefore uncovering an outbreak (Kanagarajah *et al.*, 2018). Without the use of WGS it is likely that these small or 'slow-burning' outbreaks would have persisted for longer or never been detected, demonstrating one of the clear advantages of using WGS.

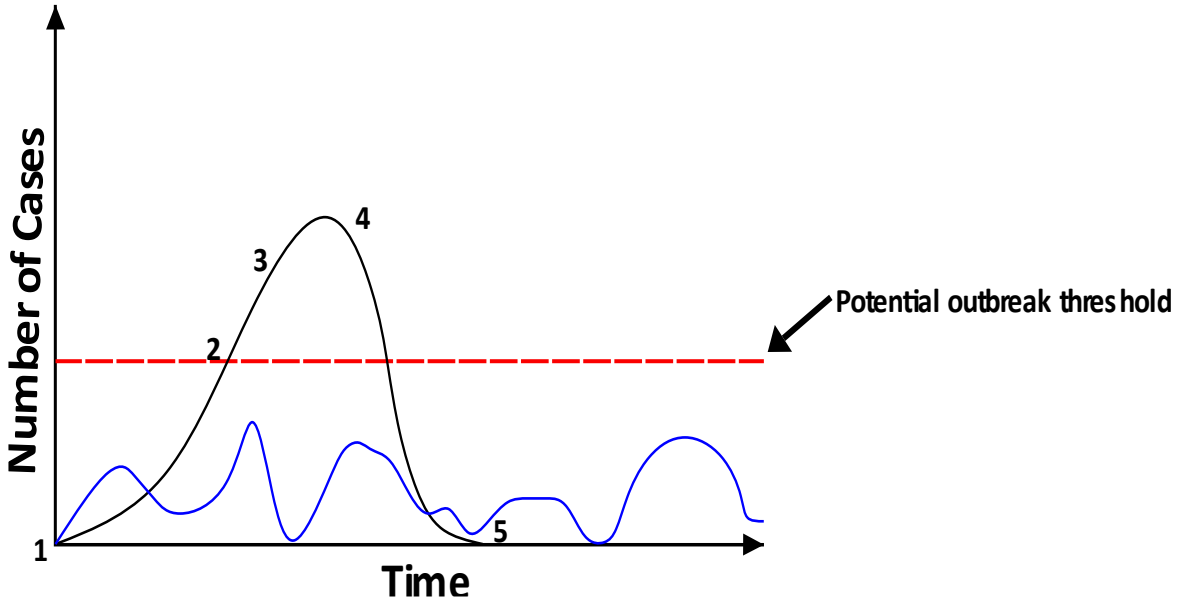


Figure 2.3: The different types of outbreak. In a conventional outbreak (black line) a general trend is followed. 1: Outbreak begins and number of cases of a particular strain increase. 2: The number of strains passes a potential outbreak threshold (exceedance), triggering an alert and possible investigation. 3: Cases continue while the source is identified and interventions are put in place. 4: The infection is removed from the population, either via effective intervention or because the infected material was removed in some way e.g. all of a

contaminated food stuff was consumed. 5: The outbreak strain is no longer present in the population or returns to expected levels.

In a ‘slow-burn’ outbreak (blue line) cases can persist over a long period of time due to the presence of an undetected source. These cases happen infrequently and therefore do not pass the potential outbreak threshold; however, they persist over a considerable time period and are all related in some way. Without the use of WGS and cluster detection, outbreaks such as these are likely to go undetected.

The WGS of isolates can also be used to inform epidemiological investigations (den Bakker *et al.*, 2014), a retrospective investigation of an outbreak associated with a long term care facility identified isolates from the surrounding community that also belonged to the highly supported outbreak clade (den Bakker *et al.*, 2014). The inclusion of these isolates in the initial investigation may have helped identify the initial source of the outbreak, as these cases suggested a contaminated source outside of the care facility (den Bakker *et al.*, 2014). While the source of this outbreak was never discovered (den Bakker *et al.*, 2014), WGS did indicate a broader source than had previously been thought, as the source was initially thought to be specifically within the care facility (den Bakker *et al.*, 2014). Another outbreak detected using WGS contained isolates of multiple PTs (Inns *et al.*, 2017), had only conventional PT surveillance been employed approximately 30% of isolates would have been lost from the outbreak definition (Inns *et al.*, 2017). This would most likely have slowed detection of the outbreak and made a food chain investigation more complicated, as clustering would have been reduced (Inns *et al.*, 2017). Furthermore, isolates that had been excluded from an outbreak investigation because they had distinct PFGE profiles should have been included in the analysis, as WGS showed that they were highly

related to the outbreak cluster (den Bakker *et al.*, 2014). The detection of more outbreaks does, however, lead to an increased workload for health protection teams and it is likely to become necessary to develop a strategic plan to balance the investigation of small localised clusters with the limited human resources available (Mook *et al.*, 2018).

2.2.3 Novel tools for *Salmonella* cluster identification

Determining clusters of related isolates which need to be investigated can be automated through the development of tools and systems, this would reduce the time taken to conduct an analysis. Novel approaches to clustering *Salmonella* isolates have been developed that appear to create unique profiles for each outbreak by using prophage genes (Mottawea *et al.*, 2018). Multiple databases have also been created that enable the typing of *Salmonella* isolates into their respective serovars and can then cluster isolates using either wgMLST (Liu, Chen and Chiou, 2016; Liu, Chiou and Chen, 2016) or whole genome SNPs (Tsai, Liu and Soo, 2017). These databases are available online and remove the need for setup of in-house typing systems (Liu, Chen and Chiou, 2016; Tsai, Liu and Soo, 2017). Analysis of the best methods for searching large-scale sequence databases to accurately determine the genetic relatedness among a set of samples have also been undertaken and the utility of the MLST approach was demonstrated, although these approaches could require considerable computing power (Pettengill *et al.*, 2016).

2.3 Outbreak investigations of *Salmonella*

2.3.1 Novel approaches to investigation using WGS

The increase in the amount of information obtained through using WGS is considerable, as WGS produces far greater quantities of genetic information than biochemical methods, phage typing, CRISPR, PFGE etc., which rely on a subset of genes (Maiden *et al.*, 1998; Bender *et al.*, 2001). This increase in genetic information in turns led to an increase in the number of clusters of *Salmonella* that are detected and may require epidemiological investigation (Waldram *et al.*, 2018), particularly in homogenous serovars such as serovar Enteritidis, where a combination of conventional approaches such as PFGE, MLVA and phage typing was still not adequate for the detection of all clusters (Ziebell *et al.*, 2017; Vincent *et al.*, 2018). PHE employed a SNP typing scheme for cluster detection of *Salmonella* serovars (Ashton *et al.*, 2016), which clustered *Salmonella* at increasing levels of SNP profile similarity in order to determine the genetic relatedness of isolates (Ashton *et al.*, 2016).

Other SNP-based workflows have also been published and validated, which demonstrated reproducibility and reliability (Portmann *et al.*, 2018). SNP pipelines have validated for phylogenomics for the analysis of *Salmonella* (Petkau *et al.*, 2017). SNP phylogenomics pipelines could also distinguish between outbreak and non-outbreak isolates across various sequencing-coverage thresholds and in the presence of contamination (Petkau *et al.*, 2017). Combinatorial approaches have also been employed for outbreak investigations, which employed SNP counts combined with phylogenetic tree topologies and bootstrap support (Pightling *et al.*, 2018). Some

databases developed for serovar identification and cluster detection have also employed wgMLST instead of SNPs (Liu, Chen and Chiou, 2016; Vincent *et al.*, 2018).

One approach which appeared to be growing in popularity for detection and investigation of genetically related clusters wascgMLST (Simon *et al.*, 2018; Vincent *et al.*, 2018). Cluster detection using cgMLST was also highly discriminatory (Simon *et al.*, 2018; Vincent *et al.*, 2018). The use of cgMLST in outbreak analysis has been shown to help elucidate temporal and geographical relationships between isolates (Simon *et al.*, 2018) and could therefore be used to aid in food traceback analyses (Simon *et al.*, 2018). The *Salmonella* cgMLST scheme was reference free and applicable to all serovars, this removed the need to develop new databases for outbreaks of rare serovars and removed concerns over the reference altering the distances between isolates (Saltykova *et al.*, 2018). Another benefit of cgMLST was that the scheme was easily transferable through online systems, allowing for easier cross-country reporting and investigation of outbreaks (Simon *et al.*, 2018), this has made it the candidate for PFGE replacement by PulseNet (Nadon *et al.*, 2017).

Reference-free WGS through phylogenetic analyses has also been examined as a novel approach for the analysis of outbreak and was also more discriminatory than PFGE (Oakeson *et al.*, 2018); however, there was some conflict between this approach and SNP typing, as a SNP pipeline included some isolates that the WGS-tree excluded, although the reasons behind this were unclear, as the original SNP tree and analysis were no longer available for further investigations (Oakeson *et al.*, 2018).

A major drawback to WGS is the time it has taken to prepare and sequence an isolate, for example Hiseq can take approximately four days, however results have been obtained in a timeframe suitable for surveillance (Taylor *et al.*, 2015). For instance, Rapid Miseq sequencing reduced the time taken to identify isolates compared with standard sequencing protocols (Quick *et al.*, 2015); however quality was reduced and some information was lost, which can reduce accuracy (Quick *et al.*, 2015). More recent sequencing technologies such as MinION (Lu, Giordano and Ning, 2016) could provide the solution to the current delay in pathogen identification and subsequent investigation. MinION sequencing was evaluated in a hospital outbreak of serovar Enteritidis and was able to produce clinically relevant information in real time (Quick *et al.*, 2015). It was able to identify the species within 20 minutes, serovar in 40 minutes and isolates were identified as a member of the outbreak clade in less than 2 hours (Quick *et al.*, 2015), although the error rate was very high in MinION analyses (Quick *et al.*, 2015) and so data needed to be treated with caution. It would therefore be possible that an isolate that had met the epidemiological inclusion criteria would be excluded, as it didn't cluster genetically due to errors.

2.3.2 Investigation of *S. enterica* outbreaks using WGS

WGS has been used for the investigation of outbreaks of *S. enterica* from all over the world, including Asia (Yan *et al.*, 2015), Oceania (Thompson *et al.*, 2017; Lindsay *et al.*, 2018), Europe (Gymoese *et al.*, 2017; Brandwagt *et al.*, 2018), North America (Hassan *et al.*, 2018; Venkat *et al.*, 2018) and South America (Byrne *et al.*, 2014). The analysis of outbreaks using WGS revealed several key advantages over phenotypic methods, phage typing, PFGE and MLVA when performing epidemiological analyses: there was increased resolution over these methods (Octavia *et al.*, 2015; Lindsay *et*

al., 2018); outbreak cases can be identified with a higher degree of certainty, enabling the inclusion or exclusion of some isolates (den Bakker *et al.*, 2014; Octavia *et al.*, 2015; Gymoese *et al.*, 2017); putative cases that match the case-definition can be ruled out of an outbreak with a higher degree of certainty (den Bakker *et al.*, 2011); and it could be possible to link or reject potential outbreak sources to isolate clusters through sequencing samples taken at potential sources and determining if any are closely related to the isolate cluster (Octavia *et al.*, 2015; Gymoese *et al.*, 2017).

2.3.3 Increased resolution within *S. enterica* outbreaks

The increased resolution of WGS can reveal previously unidentified diversity within an outbreak (Octavia *et al.*, 2015); using WGS it was possible to demonstrate that multiple strains of serovar Typhimurium had been involved an outbreak, suggesting that the source had also been contaminated with multiple strains (Octavia *et al.*, 2015). This was not observed when using MLVA, however, as all isolates shared the same MLVA profile (Octavia *et al.*, 2015). Furthermore, the increased resolution provided by WGS was particularly useful when analysing highly homogenous serovars such as serovar Heidelberg. Two serovar Heidelberg outbreaks were indistinguishable using previous outbreak analysis methods, as they shared the same PFGE pattern and the same PT (Bekal *et al.*, 2016). Analysis using WGS was able to demonstrate that these two outbreaks were genetically distinct (Bekal *et al.*, 2016), which supported the previous epidemiological conclusion that they were separate outbreaks (Bekal *et al.*, 2016).

In an outbreak of serovar Paratyphi B the opposite problem occurred and multiple PFGE patterns were observed (Hassan *et al.*, 2018); using WGS it was possible to

determine that these isolates were genetically related to each other and part of the same outbreak (Hassan *et al.*, 2018). Furthermore, a WGS analysis of multiple suspected outbreaks of serovar Choleraesuis in pig populations determined that isolates from a 1999 outbreak were considerably different from those obtained in 2012 – 2013, suggesting the outbreaks were the result of multiple infections and not due to a persistent infection (Pedersen *et al.*, 2015).

2.3.4 Identification of outbreak cases with a higher degree of certainty

The use of WGS in some outbreaks identified isolates which were previously believed to be sporadic as isolates that were closely related to the outbreak strain (den Bakker *et al.*, 2014; Octavia *et al.*, 2015; Gymoese *et al.*, 2017). When WGS cluster analysis was combined with epidemiological information the number of cases detected can increase, as epidemiological information is required to meet the outbreak case definition, in one circumstance an outbreak of serovar Typhimurium was increased by 107% through reanalysis using WGS (Octavia *et al.*, 2015). Five clinical isolates of serovar Agona that occurred prior to the detection of an outbreak were identified as genetically similar to the outbreak, indicating that contamination at the outbreak origin may have occurred earlier than previously believed (Thompson *et al.*, 2017). Use of WGS in surveillance enabled isolates to be linked from the beginning of an investigation via genetic relatedness rather than relying on an exceedance values. An outbreak of serovar Typhimurium used WGS from the beginning and identified an initial 21 closely related cases, which required further investigation, which potentially enabled early outbreak detection and intervention, leading to the prevention of further cases (Mair-Jenkins *et al.*, 2017).

Conversely, previous methods which have identified isolates as the same strain within an outbreak can also be excluded using WGS (den Bakker *et al.*, 2011). For example, a SNP-based WGS analysis determined that the majority of isolates suspected of being part of a multistate outbreak of serovar Montevideo through PFGE analysis were sporadic background cases (den Bakker *et al.*, 2011). In this study, creation of an assay based on a WGS SNPs analysis was used to analyse 112 isolates that had the same PFGE pattern as the outbreak isolates were analysed. Of these 112 isolates 80% were found to represent sporadic cases (den Bakker *et al.*, 2011). The use of WGS in the analysis of this outbreak was able to quickly discriminate between isolates inside and outside of an outbreak clade. Without the use of WGS many more isolates, which were presumed to be linked due to matching PFGE patterns, would have needed to be investigated for epidemiological links to the outbreak before they could be dismissed as unrelated cases. Therefore, the use of WGS saved both time and resources.

2.3.5 Identification and confirmation of outbreak source

Coupled with epidemiological investigations, WGS can be a powerful tool to aid in the identification of the source or vehicle of an outbreak (Crowe *et al.*, 2017; Morganti *et al.*, 2018), especially when the outbreak was caused by a frequently detected serovar (Morganti *et al.*, 2018). For example, specific source identification was challenging in chicken associated outbreaks due to high consumption rates of eggs and meat within the population, the complex import and export involved in the industry and the presence of many separate farms and brands (Crowe *et al.*, 2017). The use of WGS and appropriate sampling for source identification of a serovar Heidelberg outbreak that occurred in 2014 in the USA was able to determine that the outbreak strain had

originated from a specific producer (Crowe *et al.*, 2017). Without the increased specificity of WGS identifying the source of an outbreak within this complex environment would have been challenging. In an outbreak of serovar Give, which occurred in 2016 in Malta, epidemiological investigations coupled with WGS determined the source was most likely the cross-contamination of raw and ready to eat foods at a manufacturer; however source determination may not have been possible without WGS (Donachie *et al.*, 2018). Two potential sources, a food manufacturer and veterinary samples, were identified but initial hypotheses believed these isolates to be linked in one large outbreak, however they were found to belong to different genetic clusters that were circulating concurrently in Malta when WGS methods were applied (Donachie *et al.*, 2018). Furthermore, in 2012 an outbreak of serovar Bareilly could be traced from the USA back to India through WGS as isolates shared the same isolates formed a unique SNP cluster and could be epidemiologyically linked (Hoffmann *et al.*, 2016). Notably the closest neighbour to the outbreak clade, varied by only a few SNPs and was a strain identified nine years previously that had originated from a site 8 kms away from the Indian site implicated in this outbreak (Hoffmann *et al.*, 2016). The identification of the source of this outbreak, particularly across borders and the identification of a closely related non-outbreak strain were clear demonstrations of the utility of WGS for cluster detection and source identification in epidemiological investigations.

If the source of an outbreak is believed to have been identified through epidemiological investigation, then WGS can be used to confirm these findings. A serovar Bovismorbificans outbreak in 2014 in the Netherlands was linked to ham products from a specific retail chain, a collected sample of this ham tested positive for serovar

Bovismorbificans and matched outbreak strains using WGS, helping to confirm that the ham was the source of the outbreak (Brandwagt *et al.*, 2018). In the UK in 2015, epidemiological investigations identified a restaurant as the source of a persistent serovar Typhimurium outbreak, however identification of the pathogen reservoir within the restaurant was initially difficult (Mair-Jenkins *et al.*, 2017). Eventually the swabbing and sequencing of multiple surfaces within the restaurant was able to elucidate the drains as the pathogen reservoir (Mair-Jenkins *et al.*, 2017). Similar results were observed within an outbreak of serovar Isangi in China in 2016 where WGS was used to help confirm that the infection vector was steamed fish and mixed food or possibly one cross-contaminated the other, as samples taken from the food were highly related to outbreak isolates (Li *et al.*, 2017). This demonstrated that the regulatory guidance (not provided) on rural banquets in China should be adhered to and possible reminders may need to be issued (Li *et al.*, 2017).

WGS can also be used to rule out potential outbreak sources. For example, a live vaccine of serovar Gallinarum used in poultry flocks had been suggested as a source of outbreak within chickens in Brazil between 2011 and 2014; however, WGS was able to confirm that the outbreaks within the study period were caused by unrelated strains of serovar Gallinarum and were not related to the vaccine (Koerich *et al.*, 2018). In a serovar Give outbreak it was also possible to rule out veterinary isolates as an outbreak source (Donachie *et al.*, 2018).

2.3.6 Multinational outbreaks analysed using WGS

The detection and investigation of outbreaks across borders is complicated (Harbottle *et al.*, 2006), as it requires considerable cooperation and communication among multiple agencies across different countries. This is further complicated by the highly standardised approaches required for accurate PFGE typing (Swaminathan *et al.*, 2001) and the lack of a global PFGE database (Nadon *et al.*, 2017). WGS analyses is believed to be better suited for analyses across borders and should therefore be capable of simplifying this complex process (Nadon *et al.*, 2017).

Multiple examples of multinational outbreaks investigated using WGS now exist (Byrne *et al.*, 2014; Inns *et al.*, 2015, 2017; Fonteneau *et al.*, 2017; Pärn *et al.*, 2017). An outbreak of serovar Newport associated with watermelon from Brazil occurred from October 2011 – January 2012 and cases were identified from a number of different European countries (Byrne *et al.*, 2014), WGS was used on a subset of isolates within this outbreak to confirm the results of the PFGE analysis (Byrne *et al.*, 2014). The main advantage of WGS within this outbreak was the increased clarity it provided (Byrne *et al.*, 2014). Using WGS it was possible to determine the relatedness of the outbreak strain and other serovar Newport strains circulating within Europe (Byrne *et al.*, 2014). This analysis demonstrated objectively that the Newport strains were not closely related, helping to confirm the conclusions of the traceback investigation that the strain was imported (Byrne *et al.*, 2014). WGS has been used to confirm the identity of strains typed through biochemical methods and epidemiological tracking in a number of other multi-national outbreaks (Inns *et al.*, 2015; Fonteneau *et al.*, 2017; Pärn *et al.*, 2017). As with the multi-country serovar Newport outbreak, other multi-country outbreaks of serovar Enteritidis were able to provide additional support for the

epidemiological tracking of outbreaks (Inns *et al.*, 2015; Pärn *et al.*, 2017). In a 2014 serovar Enteritidis outbreak related to a German egg company the use of WGS revealed that multiple strains of Enteritidis, all related to the same egg producer, were all present within the outbreak (Inns *et al.*, 2015; Loman *et al.*, 2016). Furthermore, specific strains were responsible for local outbreaks within the larger outbreak, for example one cluster was responsible for an outbreak in one specific restaurant (Inns *et al.*, 2015; Loman *et al.*, 2016). In an analysis of a multinational travel associated outbreak of serovar Chester in 2014 PFGE typing identified that the source of the outbreak was in Morocco, while WGS suggested that multiple sources within Morocco could be implicated within the outbreak, including consumption of seafood, chicken sausage and turkey meat (Fonteneau *et al.*, 2017). In 2015 WGS was used in another multi-country outbreak of serovar Enteritidis in Spain and the UK demonstrating how WGS has changed how outbreaks are managed and investigated (Inns *et al.*, 2017). Prior to WGS it was accepted practice within PHE to exclude cases with travel history when examining an infectious intestinal disease outbreak in order to focus on in-country exposures. The uptake of WGS and the collection of extensive travel histories has, however, provided information on which other countries may have had cases from the same source (Inns *et al.*, 2017).

2.3.7 Serovar Enteritidis PT14b outbreak: WGS analysis of one outbreak

In 2014 a large multinational outbreak of serovar Enteritidis PT14b occurred, the cause of which was eggs from a German producer (Inns *et al.*, 2015). Over 350 cases were reported in the UK, Germany, Austria, France and Luxembourg (European Food Safety Authority, 2014), cases were initially reported as occurring from May to September, although some cases were detected until November 2014 (Inns *et al.*,

2015; Loman *et al.*, 2016). As this outbreak occurred shortly after PHE had implemented WGS for all presumptive *Salmonella* isolates (Loman *et al.*, 2016) and has a complex nature (Inns *et al.*, 2015; Loman *et al.*, 2016), it has been used in a considerable number of WGS analyses. WGS enabled the analysis of outbreaks to a much higher degree of resolution than ever before. This was particularly true of the analysis of complex multi-national outbreaks, such as this one. WGS was used in the detection, investigation and characterisation of this outbreak.

WGS was performed on isolates from infected individuals, implicated UK premises and German eggs (Inns *et al.*, 2015; Loman *et al.*, 2016). As WGS was conducted in 'near real-time' it was possible to use it to help inform public health control measures (Inns *et al.*, 2015). Part of this outbreak occurred within a hospital within the UK (Loman *et al.*, 2016), these isolates underwent rapid WGS using MinIon, which was capable of determining that isolates were part of the outbreak in less than two hours (Quick *et al.*, 2015). The speed with which this data was obtained could help to influence infection control and enabled rapid epidemiological linking of these isolates (Quick *et al.*, 2015). The use of WGS also enabled linkage, with a higher degree of certainty, of locally detected clusters of serovar Enteritidis which matched the case definition with the larger national outbreak (Mook *et al.*, 2018). This was possible as SNP based clusters corresponded at the local and national levels with very low degrees of difference (Mook *et al.*, 2018).

A SNP-based analysis of the genome sequences produced by PHE was also used in the characterisation of the outbreak and was able to demonstrate that isolates were

highly related (Loman *et al.*, 2016). The results of this SNP-based analysis, coupled with food traceback, provided strong evidence for the source of the outbreak being eggs from a German producer (Inns *et al.*, 2015). Using WGS-based analyses for investigation it was possible to show, with a high degree of statistical certainty, that within the UK the outbreak matched the distribution network of eggs from the German producer (Loman *et al.*, 2016). WGS provided a deeper insight into the genetic relatedness of isolates, which when combined with epidemiological data provided a level of insight not achievable with PFGE, MLVA, phage typing etc. (Loman *et al.*, 2016). The combination of epidemiological information and the results from WGS-based analyses enabled the linkage of sub-clusters within the outbreak to specific premises of the egg producer (Hörmansdorfer *et al.*, 2017). Furthermore, the use of WGS in this outbreak supported the successful prosecution of a restaurant that was found to be the source of infection for fifteen cases (Chatt *et al.*, 2017), as it possible to demonstrate a high degree of relatedness between the case samples and food and environmental samples taken from the restaurant (Chatt *et al.*, 2017).

Analysis of SNP-based clusters of *Salmonella* since 2014 has demonstrated the usefulness of WGS-based analysis for outbreak analysis (Waldram *et al.*, 2018). One of these SNP clusters was associated with this multinational PT14b serovar Enteritidis outbreak (Waldram *et al.*, 2018). Initially, cases in four of the serovar Enteritidis sub-clusters were not linked to the outbreak investigation as they occurred outside of the investigation criteria (Waldram *et al.*, 2018). Using WGS, however, it was possible to link all of these cases to the contaminated eggs from the German producer (Loman *et al.*, 2016; Waldram *et al.*, 2018). These sub-clusters were also associated with different sources of infection within the same questionnaire, such as eating chicken at

home and eating out (Waldram *et al.*, 2018). This level of resolution and the linkage of the isolates from a local outbreak to a larger international one would not have been achievable without WGS to elucidate subclusters within the larger outbreak.

2.4 Characterisation of *Salmonella*

2.4.1 Retrospective analyses of outbreaks

Retrospective outbreak analyses can also reveal previously undetected information about an outbreak of *Salmonella* (Bloomfield *et al.*, 2017; Morganti *et al.*, 2018) and when performed in conjunction with other isolates can produce epidemiologically relevant information (Pedersen *et al.*, 2015; Wilson *et al.*, 2016). For example, a comparison of isolates from an extended outbreak (1998 – 2012) of serovar Typhimurium in New Zealand (Bloomfield *et al.*, 2017) determined that while the isolates were from a range of sources, they were highly heterogenous indicating that transmission had been ongoing between humans, poultry, bovid and wild bird populations (Bloomfield *et al.*, 2017).

A retrospective analysis of an outbreak in Italy within 2013 of serovar 4,[5],12:i:- revealed that the outbreak had begun prior to and ended after the initial definition (Morganti *et al.*, 2018). Furthermore, a retrospective analysis of a series of serovar Typhimurium outbreaks from 2005 – 2008 that were linked to a single chicken farm in Australia produced an estimate for the short-term substitution rate in serovar Typhimurium, which was faster than rates previously estimated from analyses over a longer time period (Hawkey *et al.*, 2013). Analyses such as these reveal important biological information, which can be clinically relevant. For example, ongoing transmission between distinct populations suggested interventions would have limited success in removing the outbreak strain (Bloomfield *et al.*, 2017). Retrospective analysis of isolates using WGS revealed that a short-term substitution rate for serovar

Typhimuriumwas likely to be more epidemiologically relevant for future foodborne outbreak investigations (Hawkey *et al.*, 2013).

Analysis of outbreaks in conjunction with other cases, such as an analysis of serovar Tennessee outbreak strains that were coupled with cases from a range of other sources (Wilson *et al.*, 2016), revealed previously unidentified relationships, such as several clinical cases that could be linked to specific food sources, such as contaminated peanut butter (Wilson *et al.*, 2016). In another examintation by combining information from multiple outbreaks into one study it was possible to determine that the cause of a re-emergence of serovar Choleraesuis in Danish pig herds was a new strain, and not a persistent infection (Pedersen *et al.*, 2015). These analyses helped to reveal the genetic and evolutionary diversity of serovars, which in turn can better inform the understanding of the epidemiological pathways used by some strains (Wilson *et al.*, 2016).

2.4.2 Phylogeography of *Salmonella* serovars

Investigations into the diversity of datasets of *Salmonella* isolates are also possible. These datasets often have a common link, such as country of origin, location of isolation or source niche. Using WGS can elucidate the relationships between these isolates and can be used to examine if sharing common links leads to genetic differences between these isolates (Toro *et al.*, 2016; Wang *et al.*, 2018). Many of these analyses have focused on the phylogeography of a specific serovar and therefore have looked to distinguish clades within that serovar that were

phylogenetically distinct and shared a common association, such as country of origin (Toro *et al.*, 2016; Campioni *et al.*, 2018; Graham *et al.*, 2018).

For example, analysis of serovar Weltevreden in southern coastal China revealed close phylogenetic relationships between clinical human isolates and those taken from food samples (Li *et al.*, 2018), which is indicative of contamination and potential mishandling of food when it is being prepared. Furthermore, the majority of isolates were closely related to strains from south-eastern Asia (Li *et al.*, 2018), suggesting that exchange of serovar Weltevreden isolates has occurred recently or continues to occur between these countries. Similar results are observed in an analysis of serovar Newport, where individual lineages were determined to be highly associated with North America or Asia, with indications of further continent specific clades as well (Cao *et al.*, 2013).

Due to the prevalence of serovar Enteritidis, and its relatively recent expansion in the last twenty to thirty years in some countries (Campioni *et al.*, 2018), multiple country or region-specific analyses of serovar Enteritidis have also been undertaken, including from Chile (Toro *et al.*, 2016), Brazil (Campioni *et al.*, 2018) and Queensland in Australia (Graham *et al.*, 2018). The analysis within Brazil identified a shift in the Enteritidis circulating in Brazil after 1994 to a global clade (Campioni *et al.*, 2018), while Australia specific clades are still circulating in Australia in conjunction with a global clade (Graham *et al.*, 2018) and the Chilean analysis revealed that isolates were distinct from those circulating in the USA (Toro *et al.*, 2016). A comparison of Chilean clinical isolates with isolates from other Chilean sources identified clusters that

contained isolates from all of the analysed sources, suggesting that interspecies transmission of serovar Enteritidis occurs within Chile (Toro *et al.*, 2016).

Global analyses of serovars Enteritidis (Deng *et al.*, 2014) and Paratyphi A (Kuijpers *et al.*, 2016) have also been undertaken. Isolates in these analyses were taken from multiple countries and revealed patterns of distribution that could be associated with other factors such as geography (Deng *et al.*, 2014; Kuijpers *et al.*, 2016) or source niche (Deng *et al.*, 2014). These analyses revealed previously unknown relationships between isolates at local and global levels, which can be useful for monitoring global disease and for source attribution, especially in multi-country outbreaks of *S. enterica.*

An analysis of serovar Typhi in Nigeria indicated that serovar Typhi was introduced into the country through multiple independent introductions (Wong, Holt, *et al.*, 2016) and some of these strains were related to strains from north west and central regions of Africa (Wong, Holt, *et al.*, 2016). Concerningly, while the MDR strain (H58) appeared to be missing in Nigeria, there was evidence for MDR evolving independently from the H58 strain (Wong, Holt, *et al.*, 2016). This demonstrated the need for routine surveillance of serovar Typhi, and the other salmonellae, as the separate evolution of MDR in Nigeria highlights the increasing threat of serovar Typhi to public morbidity and mortality (Wong, Holt, *et al.*, 2016). Routine surveillance enables continual monitoring of resistance and can help to inform public health interventions (Wong, Holt, *et al.*, 2016).

WGS was, however, able to demonstrate the effectiveness of a national typhoid immunisation programme in Thailand (Dyson *et al.*, 2017). The sequencing of historical isolates and comparison with modern isolates revealed that the majority of currently circulating Thai serovar Typhi genotypes were not observed prior to immunisation (Dyson *et al.*, 2017). Modern isolates were more closely related to serovar Typhi genotypes from neighbouring countries, suggesting that endemic serovar Typhi had been reduced significantly through routine immunisation (Dyson *et al.*, 2017). This clearly demonstrated the values of WGS in understanding the impact of vaccination on pathogen populations and support the use of immunisation programmes within typhoid endemic areas (Dyson *et al.*, 2017).

2.4.3 Characterisation of salmonellae from a common source

Analyses have also been performed which characterise the diversity of all salmonellae from a specific source (Bell *et al.*, 2015; Carroll *et al.*, 2017; Fashae, Leekitcharoenphon and Hendriksen, 2018). These analyses often focus on a specific source, such as cattle (Carroll *et al.*, 2017; Fashae, Leekitcharoenphon and Hendriksen, 2018) or agriculture (Bell *et al.*, 2015) within a specific region. WGS was used to examine the diversity of *Salmonella* isolates from multiple food facilities (Wang *et al.*, 2018). The results showed that if isolates were closely related they were most likely from the same factory (Wang *et al.*, 2018) but if isolates were distantly related they could be from the same or different factories (Wang *et al.*, 2018), suggesting that within food facilities the diversity of *Salmonella* is high.

In Nigeria, a diverse range of serovars were found in cattle, some of which were also found in humans, although no common clonal cluster was found between them, suggesting that there was no evidence of zoonotic transmission (Fashae, Leekitcharoenphon and Hendriksen, 2018). Analysis of AMR genes demonstrated that isolates were generally susceptible and resistance only occurred at low levels, with the highest being 8.9% for streptomycin resistance (Fashae, Leekitcharoenphon and Hendriksen, 2018). The levels of resistance in Nigeria are in stark contrast to those observed in New York and Washington states in the USA where many isolates were MDR and the highest level of resistance was 97.8%, for ampicillin, although many AMR genes were only present in the human isolates (Carroll *et al.*, 2017). AMR profiles within some of the serovars in New York also showed geographical differences between the two states, while others were more homogenous (Carroll *et al.*, 2017). The monitoring of resistance is necessary to inform public health decisions and to help prevent the spread of resistant strains (Carroll *et al.*, 2017).

Tomatoes from the eastern shore of Virginia are implicated with *Salmonella* infection almost yearly, therefore long-term sampling (two years) and testing of environmental samples, from the plants, sediment and water for *Salmonella* was performed, serovars Newport and Javiana were isolated most commonly (Bell *et al.*, 2015). Serovar Newport isolates from 2010 were sequenced for comparison with clinical isolates associated with the consumption of tomatoes (Bell *et al.*, 2015). There were very few SNP differences between the clinical isolates and those sourced from the tomatoes, confirming that tomatoes were the source (Bell *et al.*, 2015). The majority of positive samples of *Salmonella* came from surface water and sediment, suggesting that the environment was a reservoir for these serovars within this area and that strains will

therefore continue to persist, as the root cause of the source could not be addressed (Bell *et al.*, 2015). These analyses can have a direct impact on public health interventions, for example stricter treatment regimes may need to be imposed within these areas and increased public awareness of the need to wash tomatoes before consumption could help to lower the number of associated cases.

Prospective analyses, such as these (Toro *et al.*, 2016; Wang *et al.*, 2018), aim to increase the understanding of the diversity of a given pathogen associated with a common factor, such as isolate source or country of origin. The resolution provided by WGS enables these analyses to draw reliable and potentially powerful conclusions from the data. Increased knowledge of the spread of a pathogen enables better routine surveillance and handling of outbreaks (Toro *et al.*, 2016; Wang *et al.*, 2018). For example, lineages which are geographically distinct may be useful for trace-back investigations of multi-country outbreaks. These analyses can also help to inform public health decisions, through informing changes in standards of practice.

2.4.4 AMR in Salmonella

AMR is a significant threat to human health and global surveillance of resistance enabled the tracking of the spread of resistance and monitoring of acquisition of new AMR genes within an area (Wong, Holt, *et al.*, 2016). In turn the increased level of knowledge on spread and acquisition of AMR genes can be used to inform public health decisions (Wong, Holt, *et al.*, 2016). WGS can provide a 'one-stop shop' solution to the characterisation of pathogens, including the monitoring of resistance (Moran-Gilad, 2017). Detection of AMR genes can be included within routine typing

using WGS without much difficulty as databases and pipelines have been developed to fulfil this role (Neuert *et al.*, 2018).

Within the salmonellae the levels of AMR present within similar sources, such as livestock and produce, can be markedly different (Carroll *et al.*, 2017; Fashae, Leekitcharoenphon and Hendriksen, 2018), as can the levels across countries or regions (Wong, Holt, *et al.*, 2016; Graham *et al.*, 2018; Morganti *et al.*, 2018). The examination of acquired AMR genes has become more common within phylogeographic analyses of serovars to better understand the spread of AMR within a region and globally (Wong, Holt, *et al.*, 2016; Graham *et al.*, 2018; Morganti *et al.*, 2018). A number of these analyses have demonstrated considerable differences between resistance levels in endemic and imported clades (Graham *et al.*, 2018). For example, 90 serovar Typhimurium isolates from across Brazil, were analysed and 39 AMR genes were identified in total, with isolates being most commonly resistant to sulphonamides (Almeida *et al.*, 2018). This emphasised the need for the monitoring and communication of AMR on a global level, to help prevent the spread of resistance into currently relatively unaffected areas.

Outbreak strains are now also being examined for AMR. For example, an outbreak of serovar Paratyphi A in Cambodia displayed pan-susceptibility to antimicrobials (Kuijpers *et al.*, 2016), whereas isolates within a Chinese outbreak were resistant to nalidixic acid (Kuijpers *et al.*, 2016). The analysis of an outbreak of serovar Typhi in Zambia revealed very high levels of MDR, with the majority of isolates containing a chromosomally translocated region that contained seven AMR genes (Hendriksen *et*

al., 2015). WGS phylogenetic analyses and comparisons of deletions within the genomes indicated that the cause of the outbreak was a single MDR clone but that other strains of Typhi were circulating concurrently (Hendriksen *et al.*, 2015). This was in keeping with previous results from Africa that have demonstrated high levels of MDR in African Typhi strains and suggested that it would be possible to use AMR profiles to analyse outbreaks if WGS linkage was not possible (Wong, Holt, *et al.*, 2016; Park *et al.*, 2018).

The levels of AMR within the salmonellae are also being monitored within specific locations (Leon *et al.*, 2018), following certain events (Olaitan *et al.*, 2015) and from certain sources (Edirmanasinghe *et al.*, 2017). An equine referral hospital in the USA performed AMR analyse on 255 clinical samples between 2007 – 2015 and found that while the majority of isolates were pan-susceptible, 25 were MDR (Leon *et al.*, 2018). Increased incidence of AMR is concerning for animal hospitals as it increases the risk of unsuccessful treatment and a zoonotic transmission can also pose a greater threat (Leon *et al.*, 2018). French pilgrims participating in the Hajj (the annual Islamic pilgrimage to Mecca) were monitored for potential acquisitions as samples were taken prior to and post attendance of the Hajj (Olaitan *et al.*, 2015). Following attendance individuals were more likely to carry a *S. enterica* infection and in two cases they were MDR (Olaitan *et al.*, 2015). Monitoring of human and poultry strains from abattoir and retail in Québec (Canada) revealed cefoxitin resistance in 57.5% of isolates, all of which were resistant to another four antimicrobials (Edirmanasinghe *et al.*, 2017). These studies demonstrate the need for understanding the epidemiology of *Salmonella* within certain locations and around certain events, in order to aid in the

prevention, control and treatment of salmonellosis (Olaitan *et al.*, 2015; Leon *et al.*, 2018).

Increasing levels of resistance within the *S. enterica* serovars is of particular concern. In serovar Typhi, extended-spectrum-beta-lactamase producing isolates (Rene S Hendriksen *et al.*, 2015) and ceftriaxone resistant isolates (Djeghout *et al.*, 2018) have been identified. The increasing number of AMR genes within serovar Typhi is concerning, particularly ceftriaxone resistance, as this is currently the drug of choice for serovar Typhi treatment (Djeghout *et al.*, 2018). MDR has also been observed in other serovars, including serovars Typhimurium (Mather *et al.*, 2013) and 4,[5],12:i:- (monophasic serovar Typhimurium) (Elnekave *et al.*, 2018). The analysis of the MDR strain DT104 of serovar Typhimurium showed that populations were largely distinct between animals and humans with limited transmission (Mather *et al.*, 2013). While serovar 4,[5],12:i:- was identified as present in swine in the Midwest of the USA and that it could be an emerging MDR clade (Elnekave *et al.*, 2018). Even more concerning was the identification of two cases of EDR serovar Senftenberg, isolated from patients in Zambia, which were resistant to nine different drug classes (Hendriksen *et al.*, 2013).

All of these analyses highlight the utility of WGS: surveillance can determine the rate of incidence and spread of resistant isolates, novel acquisitions of AMR genes can be identified and information on AMR profiles can be used to influence treatment strategies. For example, non-clinical use of narrow-spectrum penicillins in the 1950s may have aided the spread of beta-lactamase resistance, creating resistance to

ampicillin prior to its release onto the market (Tran-Dien *et al.*, 2018). The prevention of events such as these is possible through better understanding, monitoring and surveillance.

2.4.5 Virulence in *Salmonella*

WGS can be a helpful tool for the detection of virulence genes from collections of *Salmonella* isolates. *S. enterica* isolates from two separate states were analysed and the virulence genes were identified and compared across the serovars (20 serovars, including serovars Typhimurium, Schwarzengrund, Derby and Muenster) (Pornsukarom, van Vliet and Thakur, 2018). Virulence genes clustered according to serovar and there were also associations between virulence genes and the source from which isolates were obtained (Pornsukarom, van Vliet and Thakur, 2018). Within an analysis of serovar Heidelberg virulence genes the majority of virulence genes within the serovar were revealed to be common to all isolates (Hoffmann *et al.*, 2014). Outbreak strains had, however, acquired several extra virulence genes such as *sopE1* and the type IV secretion system when compared with environmental strains. This suggested that increased virulence can be achieved within a serovar through the acquisition of a single gene carried on a phage or plasmid (Hoffmann *et al.*, 2014). The increased levels of virulence seen could also potentially aid in the detection and prevention of outbreak cases as routine surveillance using WGS would be able to detect isolates with these virulence profiles and use interventions to prevent onward transmissions.

Using WGS can help to elucidate changes within the genome, such as the identification of genes that have helped serovar Typhi isolates persist when it was in a carrier state (Baddam *et al.*, 2012). The gene *shdA*, which was predicted to be involved in persistence within the intestine was identified, as were genes associated with Vi antigen expression, which was a well-known virulence factor (Baddam *et al.*, 2012). Ten of the SPIs were also identified, including SPI-1 and SPI-2 which enabled uptake and invasion of *Salmonella* within the host (Baddam *et al.*, 2012). The differences within the serovar Paratyphi B (and related eBurst group isolates), which alter the invasiveness of the serovar were also examined using WGS (Connor *et al.*, 2016). A cluster comprised of the more invasive strain *d*Ta^{-} showed a significant difference in the rates of invasive disease caused, although invasion did occur outside of the *d*Ta^{-} negative clade (Connor *et al.*, 2016). More invasive isolates appeared to have differences in a small number of genes, including the loss of one gene (*steB*) which was also missing in serovar Typhi (Connor *et al.*, 2016). Isolates of serovar Dublin, from across more than twenty years and over ten countries, which had been identified as clinically invasive or non-invasive were also examined. A set of virulence factors that appeared to increase the virulence of serovar Dublin isolates, in human infections was identified, as the majority of clinical isolates carried a larger virulence plasmid with more virulence genes, than isolates sampled from cattle (Mohammed *et al.*, 2017).

WGS also revealed differences between genomes and helped to identify strains which have acquired higher levels of virulence. Analysis of serovar 9,12:l,v:− using WGS found that this serovar carried the metabolic genes: beta-glucuronide operon and the *ydj* island, which were uncommon in *Salmonella* but lacked several metabolic clusters

frequently seen in *Salmonella*, including the allantoin catabolism, the inositol cluster and the mannose phosphotransferase system (Marzel *et al.*, 2014). Furthermore, additional adhesion factors were identified within isolates from Israel including PilV-like adhesin, and previously identified typhoid-associated virulence genes were also identified (Marzel *et al.*, 2014). It was possible that the presence of this unique virulence profile contributed to the high proportion of extraintestinal infections associated with serovar 9,12:l,v:− in Israel from 1995 – 2012, which indicated the potential presence of a geographically restricted highly pathogenic strain of serovar 9,12:l,v:− (Marzel *et al.*, 2014). Comparison of virulence genes in isolates associated with two powdered milk-associated outbreaks – serovars Ealing and Anatum revealed that the SPIs 1 – 5 were present in almost all of the isolates examined (Gunn *et al.*, 2016). Interestingly though, specific proteins were found to be more diverse than expected when compared to the reference and this included proteins with roles in virulence and intercellular survival (Gunn *et al.*, 2016). This suggests that higher diversity within these proteins may have impacted on the ability of these strains to cause outbreaks.

The combination of genotypic and phenotypic investigations can also identify novel relationships. For example, an outbreak clone of serovar Enteritidis within Israel was found to be superior to other serovar Enteritidis strains at replication within the macrophage when analysed phenotypically (Shomer *et al.*, 2016). WGS revealed that this strain was closely related to isolates from Canada and California, suggesting that this clone was not geographically restricted to Israel (Shomer *et al.*, 2016).

A better understanding of what makes a serovar or a strain within a serovar more virulent can help to better inform the potential risks associated with an infection. In time this information may help to inform medical interventions, for example through the creation of drugs or vaccines which specifically target these virulence-associated genes, thus creating a treatment focused on the most dangerous of infections. Furthermore, knowledge of geographically restricted virulence profiles can help to inform surveillance and the global spread of pathogens.

2.4 Conclusion

WGS has become a powerful tool for public health, which has been able to benefit many of the aspects of public health work. Within the *Salmonella* genus WGS has had an impact on how routine diagnosis was performed, for instance using WGS altered how isolates were identified and classified within some public health facilities. Combinatorial approaches were being implemented which enabled the maintenance of conventional serovar identification to be coupled with more informative genotypic classifications. Routine surveillance and outbreak investigation have been directly impacted, as WGS in combination with epidemiological investigation has been increasingly used for the detection of isolate clusters, which may form part of an outbreak and for the investigation of outbreaks. The use of WGS has impacted the resolution of outbreak investigations, provided increased certainty on involved isolates, enabled better identification of the source of an outbreak and improved the ease with which outbreaks strains can be reported and investigated across country borders. WGS can also be used to further characterise isolates that were in some way associated, for instance because they belonged to the same serovar, were from the same country, were from the same source or any combination of these factors has enabled the identification of associated lineages within the salmonellae. In turn this can aid in the routine surveillance of the global spread of *Salmonella* and inform investigations. All of these factors combined have a direct impact on the management of *Salmonella* and can be used to inform public health decisions in both routine and outbreak investigations.

Chapter Three

Comparative analysis of core genome MLST and SNP typing within a European *Salmonella* Enteritidis Outbreak

Abstract

Multi-country outbreaks of foodborne bacterial disease present challenges in their detection, tracking, and notification. As food is increasingly distributed across borders, such outbreaks are becoming more common. This increases the need for high-resolution, accessible, and replicable isolate typing schemes. Here a cgMLST scheme is evaluated for the high-resolution reproducible typing of *Salmonella enterica (S. enterica)* isolates, by its application to a large European outbreak of *S. enterica* serovar Enteritidis. This outbreak had been extensively characterised using SNP-based approaches. The cgMLST analysis was congruent with the original SNP-based analysis, the epidemiological data, and wgMLST analysis. Combination of the cgMLST and epidemiological data confirmed that the genetic diversity among the isolates predated the outbreak and was likely present at the infection source. There was consequently no link between country of isolation and genetic diversity, but the cgMLST clusters were congruent with date of isolation. Furthermore, comparison with publicly available Enteritidis isolate data demonstrated that the cgMLST scheme presented is highly scalable, enabling outbreaks to be contextualised within the *Salmonella* genus. The cgMLST scheme is therefore shown to be a standardised and scalable typing method, which allows *Salmonella* outbreaks to be analysed and compared across laboratories and jurisdictions.

3.1 Introduction

Members of the bacterial genus *Salmonella* are a major threat to human health, causing an estimated 80.3 million cases of foodborne gastroenteritis annually (Majowicz *et al.*, 2010). Diarrheal and invasive non-typhoidal *Salmonella* infections are responsible for the highest burden of all foodborne infections, causing an estimated loss of 4.07 million DALYs per year (Kirk *et al.*, 2015). *Salmonella enterica (S. enterica)* serovar Enteriditis is the largest single cause of *Salmonella* infection globally, accounting for between 40% - 60% of human cases (Galanis *et al.*, 2006; Hendriksen *et al.*, 2011) and many foodborne disease outbreaks. This serovar is particularly prevalent in Africa, Europe, North America, and parts of Asia (Galanis *et al.*, 2006; Centers for Disease Control and Prevention (CDC), 2016) and poultry and poultry products, including eggs, are the principal human infection source (Velge, Cloeckaert and Barrow, 2005). Eggs contaminated by serovar Enteritidis phage type 14b caused a large outbreak of disease, comprising over 350 cases, from May to September 2014 in multiple countries including United Kingdom, Germany, France, Austria and Luxembourg (Inns *et al.*, 2015; Dallman *et al.*, 2016).

The 2014 outbreak exemplifies the public health challenges posed by multi-national disease outbreaks (Deng *et al.*, 2013; Kinross *et al.*, 2014; Chatt *et al.*, 2017) that are a consequence of the widespread trade of food and other goods across borders (van Belkum *et al.*, 2007). Such outbreaks present difficulties in their detection, description, and resolution, as most disease surveillance occurs at the national level (van Belkum *et al.*, 2007), which makes the uniform characterisation of disease-associated isolates in different jurisdictions essential. The first broadly accepted *Salmonella* typing

scheme, the Kauffmann-White scheme, was based on the serological detection of somatic and flagella antigens (Grimont and Weill, 2007). This scheme facilitated international communication and comparison due to annual updates and maintenance by the WHO coordinated reference laboratory, located at the Insitut Pasteur (Paris, France); however, serotyping does not always reflect the genetic relatedness of *S. enterica* lineages (Harbottle *et al.*, 2006; Sangal *et al.*, 2010). For example, the serovar Newport, is associated with several genetically distinct lineages, at least two of which have distinct antimicrobial resistance profiles and different host specificities (Sukhnanand *et al.*, 2005; Harbottle *et al.*, 2006; Sangal *et al.*, 2010). In addition, although there are over 2500 serovars (Grimont and Weill, 2007), the scheme lacks the resolution necessary for outbreak detection and characterisation. PFGE fingerprinting provided increased resolution and achieved success with the PulseNet initiative (Gerner-Smidt *et al.*, 2006), but these data were difficult to compare among laboratories (Harbottle *et al.*, 2006) as they required highly standardised approaches (Swaminathan *et al.*, 2001) and a global PFGE database proved too complex and costly to implement (Nadon *et al.*, 2017).

Typing methods based on nucleotide sequence, such as MLST, have provided alternative approaches, which are scalable in resolution and the number of isolates to which they can be applied (Achtman *et al.*, 2012; Maiden *et al.*, 2013). Seven locus MLST STs can be generated with easily replicated protocols (Maiden *et al.*, 1998) and correlate well with the majority of lineages and serovars by means of eBGs (Achtman *et al.*, 2012). On the occasions that MLST is incapable of resolving genetically distinct lineages, this is a reflection of the genealogy of the species, as these lineages are often closely related or recombinant (Achtman *et al.*, 2012). Furthermore, the ST and

allele nomenclatures are internationally available and readily standardised using schemes hosted on web-based servers (Maiden *et al.*, 1998). While seven locus MLST lacks the necessary resolution for the identification of distinct outbreaks caused by closely related bacterial variants, the arrival of high throughput sequencing technologies led to increasingly affordable and practical whole genome sequence (WGS) analyses, which allowed for high-resolution isolate characterisation (Bakker *et al.*, 2011; Inns *et al.*, 2015; Quick *et al.*, 2015; Dallman *et al.*, 2016). In turn this is facilitating the adoption of WGS analyses for routine surveillance (Ashton *et al.*, 2016; Nadon *et al.*, 2017).

One means of exploiting WGS data is the identification of SNPs that vary among isolates. SNPs can be highly informative markers, which are capable of revealing evolutionary histories of homogenous groups (Octavia and Lan, 2010) and detecting and tracing outbreaks (Bakker *et al.*, 2011; Taylor *et al.*, 2015). These are detected by comparing sequence data from isolates of interest with a reference genome and nucleotides that vary within the dataset are then recorded (Bakker *et al.*, 2011). Due to inherent inaccuracies in single reads of high throughput sequencing technologies (Bakker *et al.*, 2011; Sahl *et al.*, 2015), quality assurance criteria, such as minimum coverage and distances allowed between SNPs, must be applied to ensure accuracy and consistency (Bakker *et al.*, 2011; Sahl *et al.*, 2015). Differences in these criteria, assembly pipelines and references used, can present difficulties in standardisation within and, particularly, among laboratories (Kaas *et al.*, 2014; Pightling, Petronella and Pagotto, 2014), complicating the establishment of a consistent nomenclature. Despite these difficulties, SNP-based analyses have been successful in resolving

outbreaks, including the multi-country PT14b outbreak (Inns *et al.*, 2015; Dallman *et al.*, 2016) discussed here.

An alternative approach is to upscale the MLST concept (Maiden *et al.*, 1998) to include many more loci (Maiden *et al.*, 2013). An advantage of this approach is that, as with MLST, loci used in the schemes are readily maintained and shared among laboratories using online databases such as EnteroBase (http://EnteroBase.warwick.ac.uk) or PubMLST (https://pubmlst.org) (Jolley and Maiden, 2010). It is possible to assemble schemes ranging from a small number of loci, such as conventional MLST (Maiden *et al.*, 1998) and rMLST (Jolley, Bliss, *et al.*, 2012; Maiden *et al.*, 2013), which uses the 53 ribosomal genes, up to the whole genome level: wgMLST (Jolley, Hill, *et al.*, 2012; Moura *et al.*, 2016). In order to distinguish between the closely related isolates found within an outbreak (Hoffmann *et al.*, 2014; Jackson *et al.*, 2016), a large number of genes need to be included within a given scheme. Core genome schemes (Maiden *et al.*, 2013) balance the number of loci used in a scheme with the maximum possible resolution, by including those loci present in the majority of isolates (ranging from 95% - 99% (Bratcher *et al.*, 2014; Moura *et al.*, 2016)) in a given grouping of bacteria (Bratcher *et al.*, 2014; van Tonder *et al.*, 2014; Moura *et al.*, 2016). Ideally these genes reflect the true genealogy within the species and do not change presence over time (Moura *et al.*, 2016), which makes them forward and backward compatible (Moran-Gilad *et al.*, 2015). To encourage this, elements not under strict selection pressures, such as repetitive genes and pseudogenes should be excluded during development (Moura *et al.*, 2016). Previous studies within other bacterial species have shown SNPs and cgMLST to be congruent (Hyun *et al.*, 2014; Kohl *et al.*, 2014). As with MLST and rMLST, cgMLST can form the

basis of a stable, reference free, internationally curated nomenclature scheme accessed via databases, that permit global epidemiology and other analyses (Bratcher *et al.*, 2014; Moura *et al.*, 2016).

For the purposes of this work, wgMLST is defined as a non-redundant set of genes that are present across a set of genomes representing a species, akin to a pan-genome. Consequently, a wgMLST scheme includes a greater number of genes than a cgMLST scheme and may also include highly variable elements such as repetitive genes and pseudogenes, if they are present in any included genome (Moura *et al.*, 2016).

Here the application of cgMLST for the characterisation of international outbreaks of serovar Enteritidis disease was validated by a reanalysis of the European PT14b outbreak and comparison of the results previously obtained by SNP analyses. Core genome sequencing was shown to be a viable alternative high-resolution analysis approach, which is highly reproducible and scalable. Furthermore, it was demonstrated that cgMLST can be readily implemented in laboratories that only have access to web-based bioinformatics analysis tools, which makes it of particular utility in the resolution of multi-country disease outbreaks. This is because the submission of sequence data to one database makes it unnecessary for isolate sequences to be assembled in the same laboratory and allows for the easy addition or removal of sequences from datasets.

3.2 Materials and Methods

3.2.1 Data sources

The outbreak dataset analysed here includes sequenced reads of isolates described previously (Dallman *et al.*, 2016). Sequence data were retrieved from the Sequence Read Archive (SRA) (https://www.ncbi.nlm.nih.gov/sra) and assembled using the SPAdes (Bankevich *et al.*, 2012) based assembly pipeline developed for the EnteroBase (http://EnteroBase.warwick.ac.uk) database (Appendix A).

3.2.2 Datasets

All comparative analyses were performed using isolates from the multi-country European outbreak of PT14b serovar Enteritidis, described by Inns *et al.* (Inns *et al.*, 2015) and closely related non-outbreak isolates identified previously by Dallman *et al.* (Dallman *et al.*, 2016). Several aspects of this outbreak make It particularly useful for comparing analytical approaches: it spanned several countries, occurred over several months, consisted of three distinct serovar Enteritidis clades associated with primary production and there was sub clustering of point source outbreaks. Furthermore, the availability of non-outbreak isolates that are closely related to those within the outbreak, allowed for further analyses to be performed. For all outbreak isolates the country and year of isolation were known and for most the month of isolation was also available. The outbreak associated isolates were organised into three datasets (A – C, Appendix A).

Dataset A: Consisted of the 530 isolates from the Dallman *et al.* study (Dallman *et al.*, 2016); however, three of the isolates listed within the dataset: 53063, 45270 and

48189 had identical SRA accessions as other isolates (SRR1969068, SRR1957842 and SRR1957842 respectively) and as such could not be identified within the SRA. These were excluded from the analysis, leaving a dataset of 527 isolates. This dataset contained both outbreak isolates and closely related non-outbreak isolates.

Dataset B: Consisted of the 401 isolates previously used to generate the SNP tree analysis in Dallman *et al.* (Dallman *et al.*, 2016); however, 15 isolates were removed, as they were either duplicates or not possible to identify within the SRA, leaving 386 isolates within the analysis. This dataset contained only outbreak isolates.

Dataset C: Consisted of the 193 isolates from the UK part of the outbreak which had exposures associated with several restaurants and food vendors (Inns *et al.*, 2015). Of these, eight isolates were mixed samples and a further six failed the quality controls within EnteroBase (http://EnteroBase.warwick.ac.uk), these fourteen isolates were discarded, leaving a dataset of 179 isolates.

3.2.3 Description of cgMLST and wgMLST

WgMLST and cgMLST schemes have been defined in EnteroBase, as standard genotyping methods for *Salmonella*, for improved discrimination of genotype as compared to 7-locus MLST and 53-locus rMLST schemes.

Construction of cgMLST and wgMLST schemes consisted of three stages. Firstly, coding sequences were compiled from 537 *Salmonella* genomes, including: 167

complete genomes in NCBI, 82 NCTC genomes from PacBio sequencing and 288 representatives for one genome per eBURST group (Achtman *et al.*, 2012) (based on rMLST) within EnteroBase. The rMLST eBURST groups were clusters of genetically closely related isolates (Achtman *et al.*, 2012) based on rMLST, a typing approach which uses the 53 ribosomal genes to identify and define species and their groupings (Jolley, Bliss, *et al.*, 2012; Maiden *et al.*, 2013). The genomes from the eBURST groups encompassed the genomic diversity within the *Salmonella* genus and consisted of a total of 2,406,798 CDS, which were grouped into 75,864 gene clusters using Uclust (Edgar, 2010). In order to identify homologous regions within each genome, the centroid sequences of each clusters were aligned onto all 537 genomes using nucleotide BLAST, where a gene was considered present if a match covered greater than 70% nucleotide identity over 50% of the length of the centroid sequences.

Paralogous genes (or paralogs) are homologous genes where a gene duplication event has occurred, followed by parallel evolution (Fitch, 1970). The sets of homologous regions with potential paralogs were identified if they were duplicated within any single genome. These regions were iteratively sub-clustered based on phylogenetic topology, firstly each set of sets of homologous regions were aligned together. Then the resulting alignment was used to generate a Maximum likelihood tree using FastTree (Price, Dehal and Arkin, 2010) and the ETE3 (Huerta-Cepas, Serra and Bork, 2016) python package was used to bipartition the tree to maximise the nucleotide diversity (at least 5%) between the subtrees. Each of the resultant subtrees was evaluated iteratively until no two regions came from the same genome

in the same subtree, or the maximum inter-subtree diversity was less than 5%. Then the original set of homologous regions was replaced with all of its sub-trees.

After the division process, all the homologous sets were scored and ranked according to the summarised alignment scores of their homologous regions. Homologous sets were discarded if they had regions that overlapped with the regions within other sets that had greater scores. Finally, a complete set of 28,883 ‘pan genes’ was identified for the 537 genomes. This set was further refined to 21,065 clusters, after similar gene clusters were merged if genes shared over 70% amino acid similarity. From each cluster, a single representative with the greatest alignment score was chosen to create a wgMLST scheme for *Salmonella*. This removed potential non-specific matches to paralogs in the downstream typing procedure. 3,258 Salmonella genomes, representing all rMLST STs in EnteroBase (up to May. 2016), were typed using this novel scheme.

To generate the cgMLST scheme, a subset of wgMLST loci was selected based on three criteria: (1) the loci were present in over 98% (3,193) of the genomes, (2) the coding frames for the loci were intact in over 94% (3,063) of the genomes and (3) the number of alleles fell within the majority of all loci. This process yielded a total of 3,002 loci, which formed the cgMLST scheme for *Salmonella* employed here.

3.2.4 Comparison of SNPs and cgMLST

SNPs and cgMLST were compared using datasets A and B. SNP data was provided by the authors of Dallman *et al.* (Dallman *et al.*, 2016) and cgMLST results were

derived using the *Salmonella* cgMLST V2 scheme in EnteroBase (http://EnteroBase.warwick.ac.uk). Every new combination of alleles was assigned a new cgMLST ST, including if a locus was missing in one isolate and present in another. PHE use SNP addresses (Ashton *et al.*, 2015) as unique identifiers within a given dataset. These are calculated using hierarchical single linkage at decreasing levels of genetic differences (250, 100, 50, 25, 10, 5 and 0 SNPs different) to identify epidemiologically significant clusters (Ashton *et al.*, 2015). For the statistical comparison between cgMLST and SNP addresses the cgMLST STs were filtered for missing data and combined into single linkage clusters with one as a cut-off, which prevented missing loci from contributing to the variation of cgMLST STs. Comparison of cgMLST single linkage clusters and the PHE SNP addresses was carried out on Dataset A using Simpson's diversity index (Carriço *et al.*, 2006) and the adjusted Wallace coefficient (Severiano *et al.*, 2011). The Simpson's diversity index identifies statistically significant differences between counts of unique profiles generated by different typing methodologies. It has a value between 0 and 1, depending on the number of partitions created by a typing method and a significant difference between discriminatory abilities is determined by examining the value's 95% confidence intervals, to ensure there is no overlap. The adjusted Wallace coefficient is a quantitative measure of congruence, which calculates the statistical significance of similarities between partitions generated by different typing methods, while accounting for the possibility of agreement occurring through chance alone. It also has a value between 0 and 1 depending on the ability of a typing method to further subdivide others and accounts for 95% confidence intervals. This is to better ensure that differences in sub-division are not occurring by chance.

Further comparison of cgMLST and SNPs was performed on Dataset B using the tanglegram algorithm (Scornavacca, Zickmann and Huson, 2011), generated within Dendroscope 3 (Huson and Scornavacca, 2012). The tanglegram algorithm compares two phylogenetic networks by placing rooted trees side by side and drawing a straight line (or connector) between corresponding taxa (identified through identical tip labels). The algorithm minimises the number of crossings between connectors (Scornavacca, Zickmann and Huson, 2011), therefore if the two trees are identical no connectors will cross. Changes between the internal nodes of the phylogenies of the two trees can cause multiple short-range crosses, all in the same direction, between connectors; however, this demonstrates that clustering at the tips of the phylogeny remained the same. Distance matrices calculated for cgMLST and SNPs, respectively, were used in SplitsTree 4 (Huson and Bryant, 2006) to create the neighbour-joining trees necessary for the tanglegram algorithm. The neighbour-joining trees were then loaded into Dendroscope 3 (Huson and Scornavacca, 2012) and the tanglegram algorithm was applied.

3.2.5 Comparison of cgMLST and wgMLST: food traceback

Dataset C was used to compare cgMLST and wgMLST. Identification of all loci present within each isolate was performed using the wgMLST scheme, which is available within EnteroBase (http://EnteroBase.warwick.ac.uk). As with the comparison between cgMLST and SNPs, the comparison between cgMLST and wgMLST (Ashton *et al.*, 2015) was carried out using Simpson's diversity index (Carriço *et al.*, 2006) and the adjusted Wallace coefficient (Severiano *et al.*, 2011). Minimum spanning trees were then created within EnteroBase using both cgMLST and wgMLST (Ribeiro-Gonçalves *et al.*, 2016) and were edited using the GrapeTree function. These were

annotated using the food traceback, which was provided by PHE, and a visual comparison was performed.

3.2.6 Geographic versus temporal distribution of the isolates using cgMLST

This analysis was performed using Dataset A. Minimum spanning trees were created within EnteroBase (http://EnteroBase.warwick.ac.uk) using cgMLST and edited using the GrapeTree function. These were then annotated using the sample date and country data from Dallman *et al.* (Dallman *et al.*, 2016). For the temporal analysis, the minimum spanning tree was annotated using only the year of collection for isolates outside of the outbreak period (2012, 2015 and 2016). Isolates within the outbreak period were annotated using the month and year of collection, except in the instances where only the year of collection was available, in these cases only the year was used.

3.2.6 Placing the outbreak within the rest of Enteritidis using cgMLST

A search of EnteroBase was performed, using the built-in SISTR application (Yoshida *et al.*, 2016), for genome records that were identified as serovar Enteritidis. This returned 8,365 (Appendix B) isolates, which passed the internal EnteroBase assembly checks, and were analysed using cgMLST to generate a minimum spanning tree. The minimum spanning tree was annotated using the seven most common rMLST STs within serovar Enteritidis and the remaining isolates were grouped together under the collective term ‘other’.

3.3 Results

3.3.1 Comparison of SNPs and cgMLST: Tanglegram

The 527 unique isolates in Dataset A (Appendix A) were resolved into 249 different sequence types using the PHE SNP address (Ashton *et al.*, 2015) (Simpson's diversity index = 0.949; 95% CI: 0.937 – 0.961). In comparison, single linkage cgMLST clusters generated fewer profiles, resolving the dataset into 229 unique sequence types (Simpson's diversity index = 0.901; 95% confidence interval (CI): 0.879 – 0.923 (Carriço *et al.*, 2006)) (P <0.001). The SNP addresses therefore provided a greater resolution than cgMLST single linkage clusters (adjusted Wallace coefficient = 0.874; 95% CI: 0.808 – 0.942). Some cgMLST single linkage clusters, however, did further subdivide SNP addresses, although not as strongly as SNP addresses subdivided cgMLST linkage clusters (adjusted Wallace coefficient = 0.430; 95% CI: 0.350 – 0.507 (Severiano *et al.*, 2011)) (P<0.001). Unlike a SNP analysis, a cgMLST scheme will not include intergenic regions. Furthermore, only one allelic change will be counted when multiple nucleotides change within the same gene. On the other hand, short insertions or deletions in the core genes are ignored by many SNP analysis but captured by a cgMLST scheme, because they change the sequences of the genes. The small differences between SNP and cgMLST analyses observed here will be due to a combination of these factors.

Dataset B (Appendix A) isolates were used to generate a tanglegram (Scornavacca, Zickmann and Huson, 2011): for a visual comparison of cgMLST and SNPs, which showed good congruence between the two methods (Figure 3.1). There were some minor differences in the two phylogenies, predominantly caused by inversions of

clusters, which was explained by differences between the internal nodes, located deeper within the phylogenies. A visual comparison of the two neighbour-joining trees (Appendix C) indicated that the majority of isolates were grouped into the same clusters, whether analysed with SNPs or cgMLST.

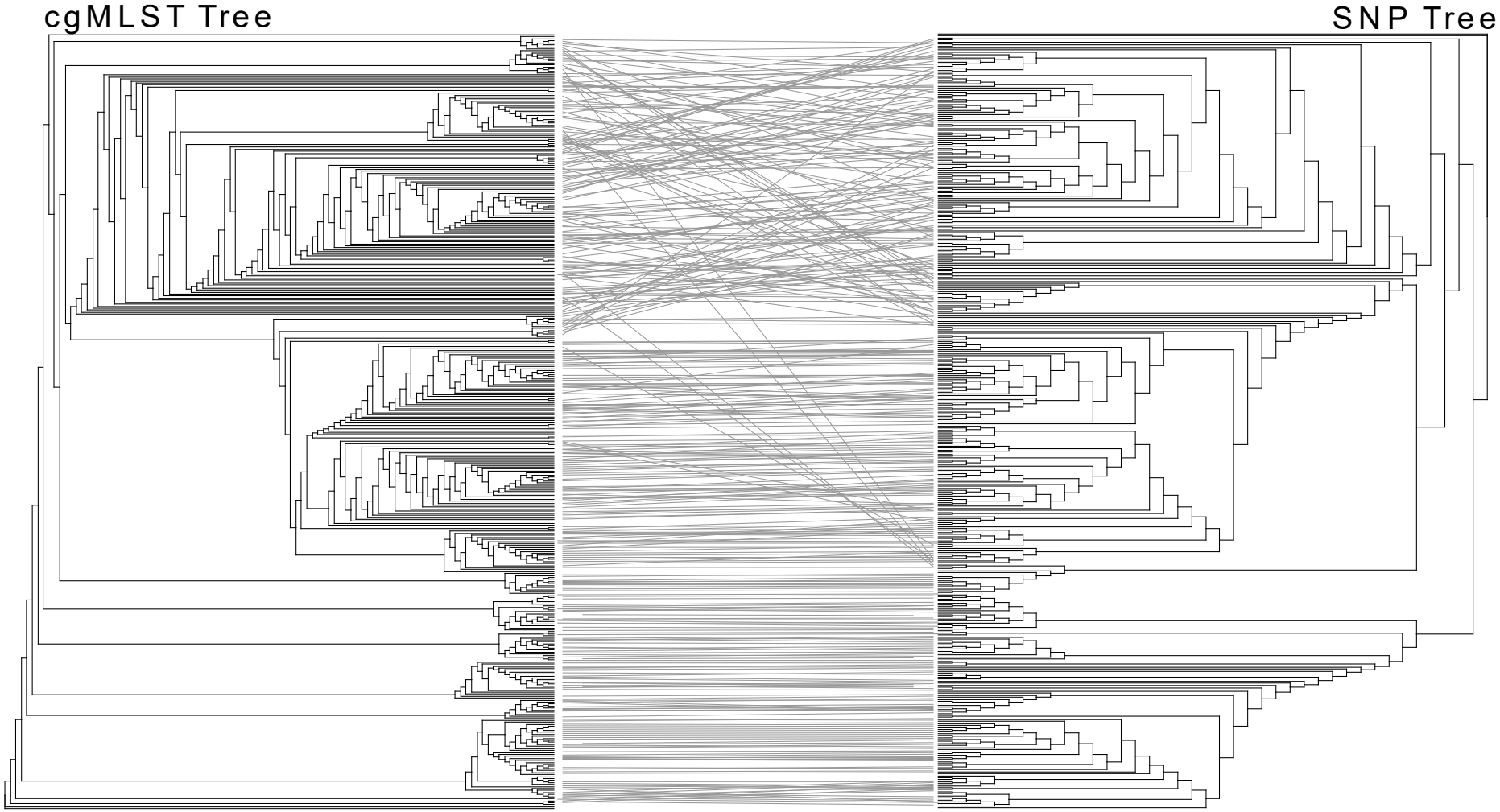


Figure 3.1: Comparison between whole genome SNP phylogeny and cgMLST in European Outbreak data.

Tanglegram (Scornavacca, Zickmann and Huson, 2011) linking tips with the same label to each other via a straight line, produced within dendroscope 3 (Huson and Scornavacca, 2012). A SNP based neighbour-joining tree (right) is compared with one generated using cgMLST (left). Clustering within the two trees was mostly congruent, although the top section of the tree showed several inversions. These inversions were caused by differences in clustering at the deeper nodes, which were not as strongly supported. This led to the positioning of some isolates, which were clustered at the edge of one tree, moving to the centre of the other.

3.3.2 Geographic versus temporal distribution of the isolates using cgMLST

The majority of the outbreak occurred from May to September 2014, with sporadic cases persisting until December and closely related isolates occurred in 2012, 2015 and 2016. The outbreak was spread across multiple countries including: United Kingdom, Germany, France, Austria and Luxembourg (Inns *et al.*, 2015; Dallman *et al.*, 2016).

The minimum spanning trees generated from Dataset A (Appendix A) showed that the majority of outbreak isolates formed one large cluster, with the sporadic cases more dispersed through the remainder of the phylogeny (Figure 3.2). However, there was no observable relationship between isolate clusters and country of origin (Figure 3.2a), suggesting that diversity did not emerge during the outbreak but was present before the start of the outbreak, as was suggested from SNP analyses (Dallman *et al.*, 2016).

When the phylogeny was analysed by the month and year of isolation, isolates from 2012, 2015 and 2016, which were closely related but did not belong to the outbreak, did not fall within the same genetic cluster as the outbreak isolates. These isolates were also diverse, suggesting that they were more genetically distant from the outbreak group and each other (Figure 3.2b). Clusters of cgMLST types within the outbreak often contained isolates from only one or two months and when a cluster consisted of multiple months they were generally consecutive. This suggested that various closely related subtypes of serovar Enteritidis replaced each other over the course of the outbreak. This was consistent with the food traceback investigations, which suggested that there were multiple point source outbreaks within the United Kingdom (Dallman *et al.*, 2016).

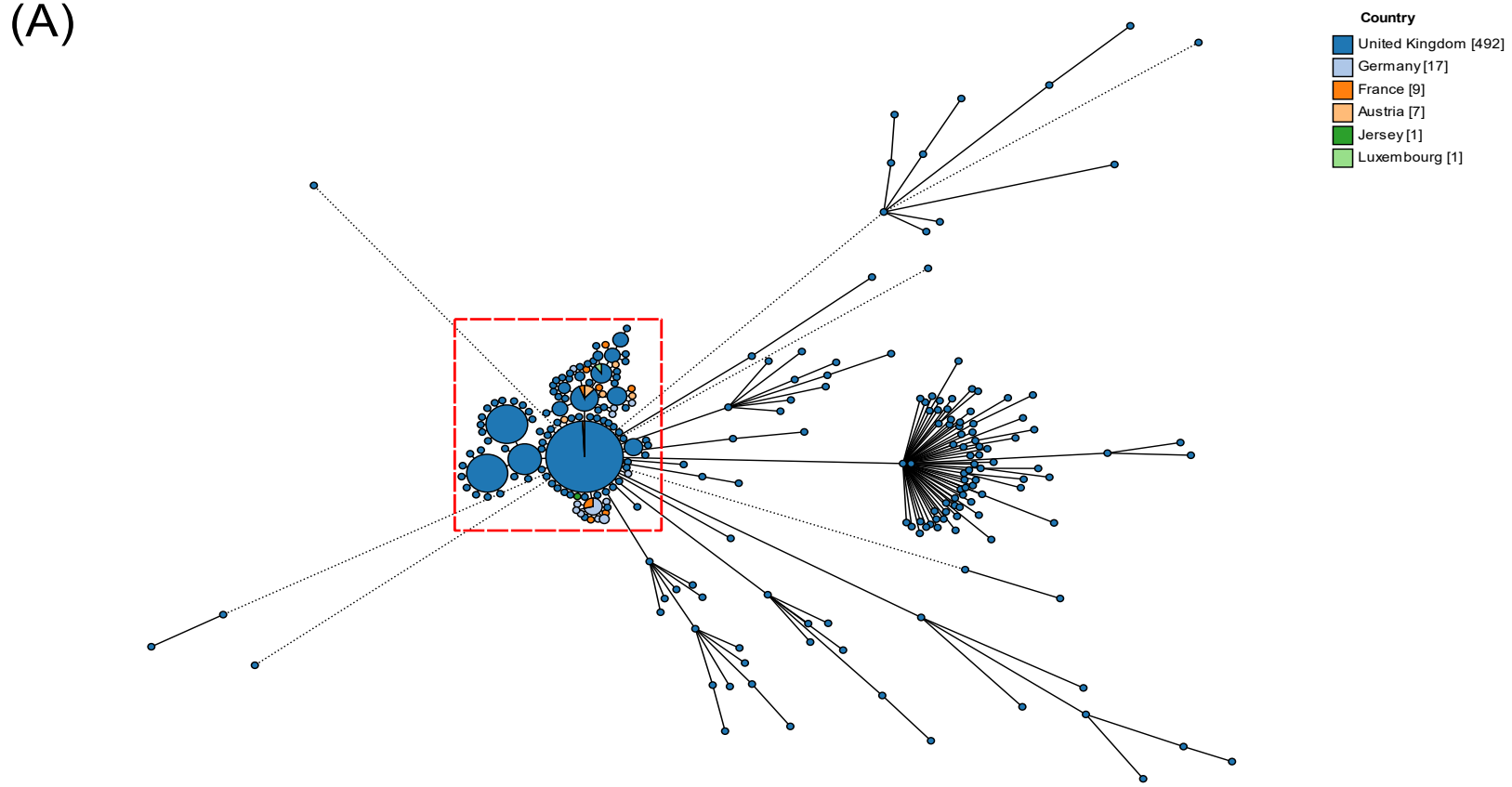


Figure 3.2 a and b: Core genome minimum spanning tree illustrating the spread of outbreak isolates based on country of origin (A) and time of collection (B). Minimum spanning tree for 527 isolates from 2012 – 2016 generated from cgMLST data, using the 3002 locus cgMLST scheme, which is available within EnteroBase. Branches longer than 301 differences were proportionally shortened and are represented by dashed lines.

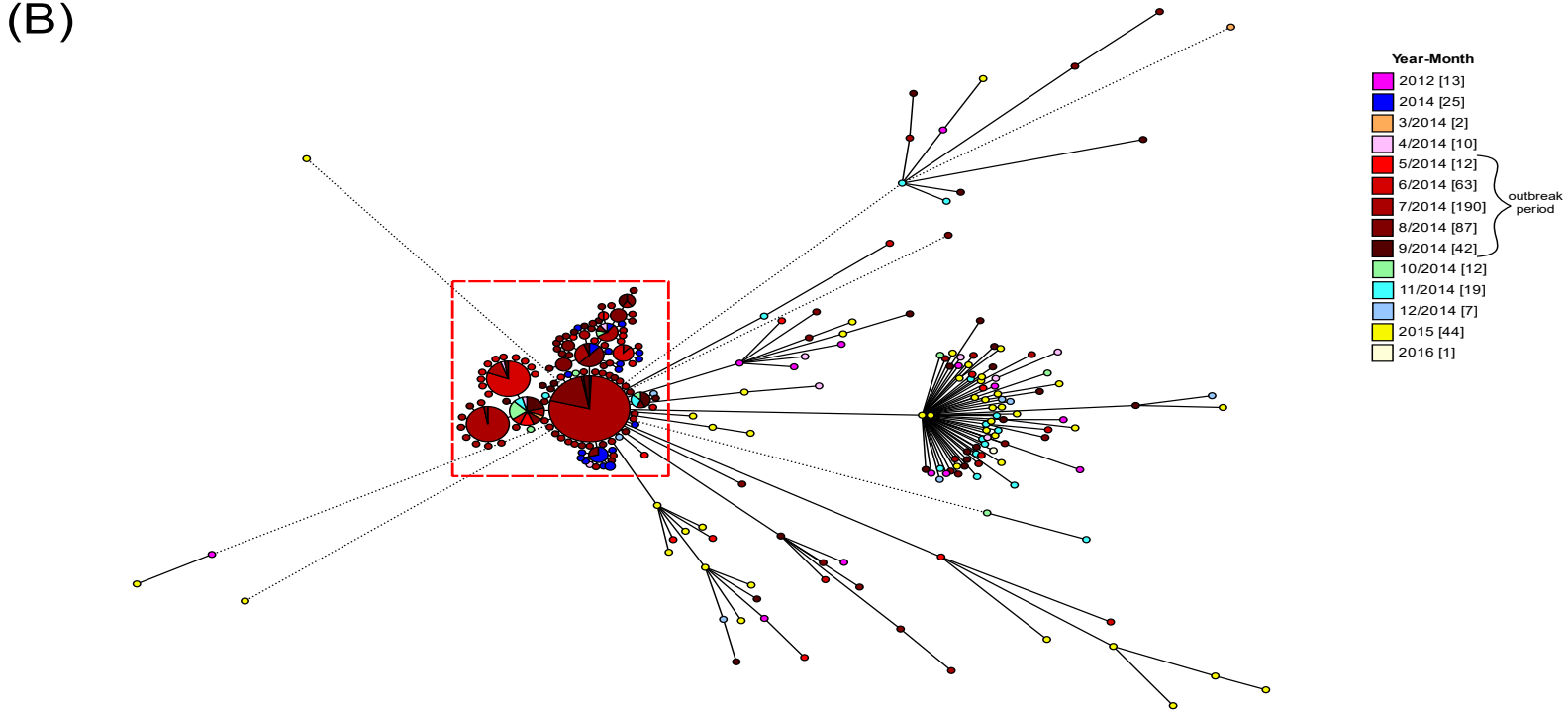


Figure 3.2 a and b: Core genome minimum spanning tree illustrating the spread of outbreak isolates based on country of origin (A) and time of collection (B). Minimum spanning tree for 527 isolates from 2012 – 2016 generated from cgMLST data, using the 3002 locus cgMLST scheme, which is available within EnteroBase. Branches longer than 301 differences were proportionally shortened and are represented by dashed lines.

A: Annotated by country: United Kingdom, dark blue; Germany, light blue; France, orange; Austria, light orange; Jersey, dark green; and Luxembourg, green (Dallman *et al.*, 2016). The majority of the outbreak (within the red box) fell within the top left cluster of the tree, while the rest of the tree was dominated by sporadic cases. This tree indicated that there was no relationship between the country of isolation and the cgMLST clusters within the outbreak, indicating that the diversity predated the outbreak.

B: Annotated by year of isolation. Most outbreak-associated cases occurred from May to September 2014, with individual cases persisting until December. As the year of most interest the months of 2014 were individually labelled, if the information was available. The outbreak months of May to September were coloured on a gradient and the remaining months of 2014 were coloured independently, while the other isolates were grouped by year: 2012, 2015 and 2016. Most of the outbreak associated isolates were clustered in the top left of the tree (within the red box) with the tree otherwise dominated by sporadic cases. This topology indicated that there was a relationship between year of infection and genetic diversity, as isolates from 2012, 2015 and 2016 predominately occurred outside of the outbreak cluster. Groups of cgMLST types within the outbreak were frequently dominated by isolates from one or two months, suggesting that different outbreak strains were dominant at different times during the outbreak.

3.3.3 Comparison of cgMLST and wgMLST: food traceback

Dataset C (Appendix A) was used to compare cgMLST and wgMLST. The 177 isolates had 177 unique wgMLST sequence types (Simpson's diversity index = 1.000; 95% CI: 1.000 – 1.000), compared with 137 cgMLST types (Simpson's diversity index = 0.981; 95% CI: 0.969 – 0.944 (Carriço *et al.*, 2006)). ($P<0.05$). Due to the larger number of distinct profiles obtained through wgMLST, it provided additional resolution compared to cgMLST (adjusted Wallace coefficient = 1.000; 95% CI: 1.000 – 1.000 (Severiano

et al., 2011)). However, there was no statistically significant difference (P =1.000) in the discriminatory ability of cgMLST and wgMLST.

These results were consistent with the results of mapping the available food traceback isolates onto minimum spanning trees (Figure 3.3). Both approaches (Figure 3.3a and 3.3b) grouped the isolates into the identical clusters of: restaurants A and H and vendor K; restaurants D, E, I and vendor L; restaurants B, C, F and G and unspecified J. Neither approach distinguished isolates on geographical source suggesting that there was no relationship between place of isolation and genetic clustering of the isolates. Furthermore, when compared with the original food traceback (Inns *et al.*, 2015) there was no relationship between clusters and the wholesalers supplying the sources, suggesting that any diversity within the isolates was generated at the source, before the outbreak began. Kingdom (Dallman *et al.*, 2016).

(A)

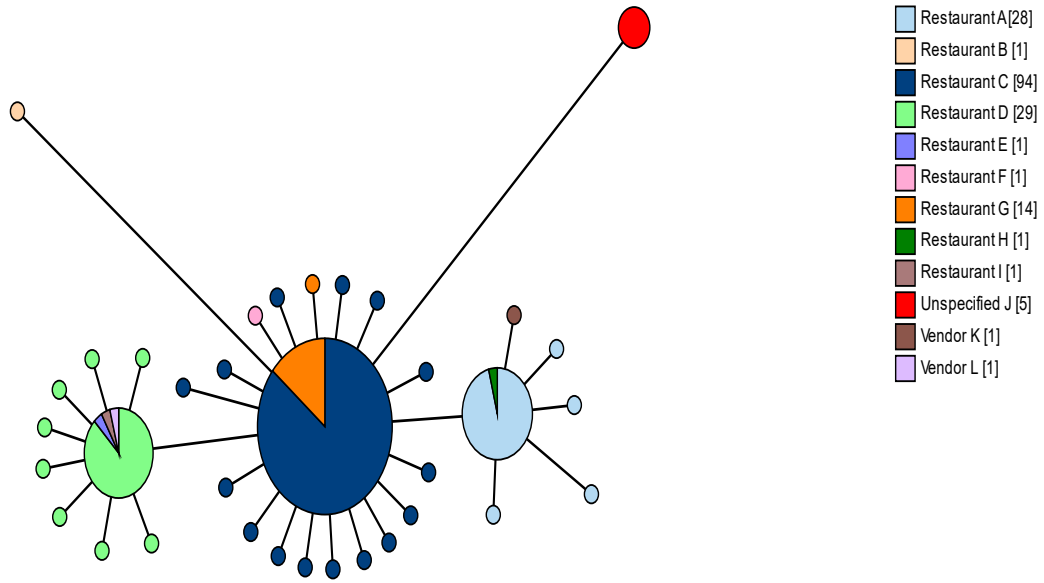


Figure 3.3 a and b: Core genome minimum spanning tree (A) and whole genome minimum spanning tree (B). minimum spanning trees of 177 unique isolates

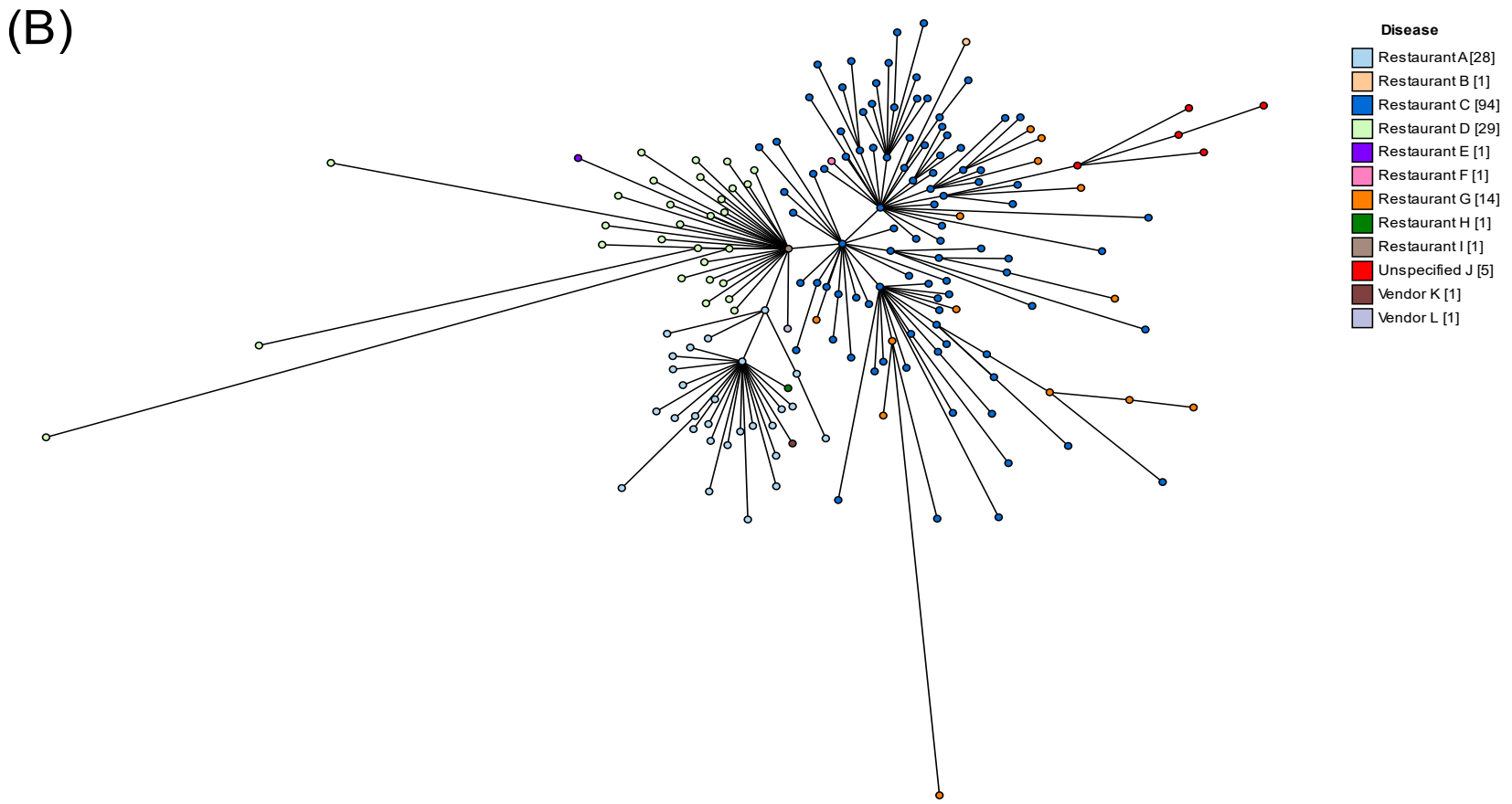


Figure 3.3 a and b: Core genome minimum spanning tree (A) and whole genome minimum spanning tree (B). minimum spanning trees of 177 unique isolates

A: calculated using the cgMLST scheme, which consists of 3002 loci and is available in the EnteroBase database.

B: calculated using the wgMLST scheme, which consists of all loci present in 100% of all of the isolates within this dataset and is available in the EnteroBase database.

3.3.4 Placing the outbreak within the rest of Enteritidis using cgMLST

Beyond being able to resolve outbreaks, cgMLST schemes are also capable of placing an outbreak into a wider context. As they use a predefined set of loci, it is possible to show the outbreak in the context of other *Salmonella* isolates, for example using all of the serovar Enteritidis isolates available within the EnteroBase database (Figure 3.4). Annotation of the isolates using rMLST showed that all outbreak isolates belonged to rMLST 3888. Despite the increased number of Enteritidis isolates, the outbreak formed an identifiable cluster within the minimum spanning tree.

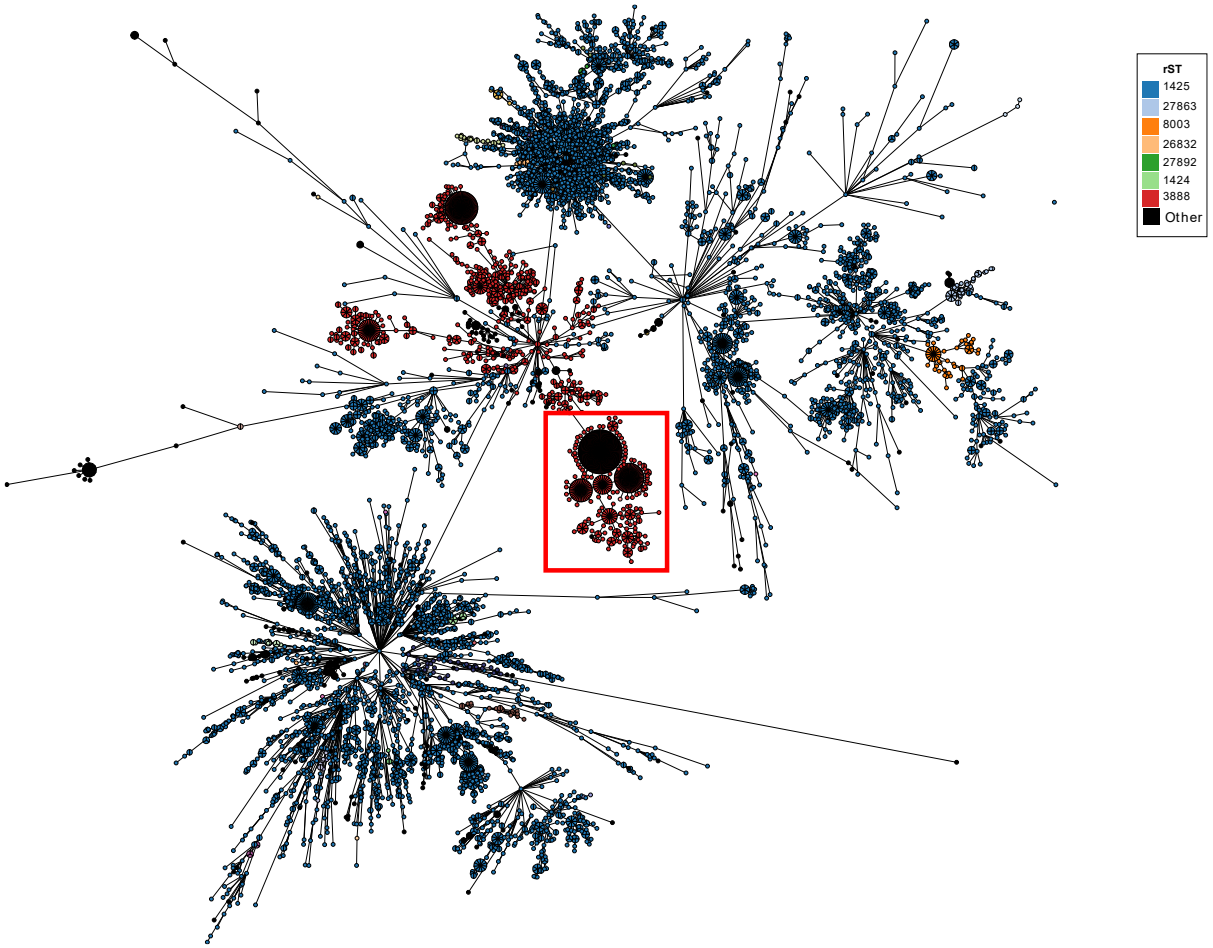


Figure 3.4: Core genome minimum spanning tree placing the outbreak within the rest of serovar Enteritidis. Minimum spanning tree, generated using EnteroBase, including genome data for all serovar Enteritidis (9,380) and PT14b outbreak isolates within the database as of December 2016. Each node, whose size is proportional to the number of isolates, corresponds to a single sequence type profile based on 3,002 core genes (cgMLSTv2, as described in EnteroBase). Nodes are colour-coded according to sequence types defined by rMLST. The Pt14b outbreak isolates (boxed in red) from a unique cluster within serovar Enteritidis diversity. All nodes are linked (black lines) sequentially to the most closely related node with the highest number of cgMLST alleles in common.

3.4 Discussion

WGS technologies provide powerful data collection and analysis techniques that can be implemented to tackle the challenges presented by the globalisation of food production and distribution. The continual transportation of foods, and therefore pathogens, across boarders requires routine high-resolution surveillance and outbreak detection methods. For the characterisation of bacterial isolates, nucleotide sequence based technologies have several potential advantages, including high throughput, reproducibility and sensitivity (Bakker *et al.*, 2011; Quick *et al.*, 2015; Dallman *et al.*, 2016). For effective implementation within a public health setting uniform nomenclatures and protocols need to be adopted. Databases such as PubMLST.org (Jolley and Maiden, 2010) and EnteroBase (http://EnteroBase.warwick.ac.uk) can facilitate global communication and collaboration by providing widely accessible nomenclature servers for multiple hierarchical MLST schemes (Maiden *et al.*, 2013), which can be used to characterise isolates, grouping and discriminating between them as required for the epidemiological application (Nadon *et al.*, 2017).

Foodborne disease outbreaks can be detected via a top-down approach, where a common source is determined, such as a restaurant or specific food product and then isolates relating to that source can be analysed. Another approach is bottom-up, where isolates are found to be sufficiently similar that they are deemed likely to be a consequence of infection from a common source, which may be identified by epidemiological investigation. While a top-down approach is easily analysed by many different typing systems, a bottom-up approach can be more difficult, especially when more than one country is involved. An advantage of gene-by-gene approaches such

as MLST, rMLST and cgMLST, is that they can be employed to make rapid comparisons of large numbers of isolates (Maiden *et al.*, 2013). Progressively increasing the resolution of these approaches, by increasing the number of loci used, allows for the identification of previously undetected disease clusters. The cgMLST schemes enable high resolution within a species or genus which can also be used as the basis of nomenclature (Maiden *et al.*, 2013; Moura *et al.*, 2016) and the usefulness of such schemes for investigation and description of outbreaks, has previously been demonstrated (Hyun *et al.*, 2014; Kohl *et al.*, 2014).

In cgMLST a set of loci, 3002 for the *Salmonella* scheme described here, is used for gene-by-gene comparisons of assembled bacterial isolates. These schemes summarise the diversity present within the nucleotide sequences of these loci, as each distinct sequence at every locus is identified as a variant. Using alleles as the basis of a comparison, instead of nucleotide sequences, accounts for differences due to single evolutionary events that introduce many polymorphisms, such as horizontal gene transfer (Moura *et al.*, 2016). An advantage of the allelic approach is that loci which differ within a comparison are obvious and the nucleotide sequences can still be accessed when necessary for any further analyses. Within this scheme only coding sequences are included, however this is not dissimilar to SNP based analyses as polymorphisms within intergenic regions are often excluded, due to low coverage or genomic complexity (Bakker *et al.*, 2011; Sahl *et al.*, 2015). While the exclusion of the accessory genome may lead to a decrease in resolution, it enables direct comparison with all members for which the scheme was established (Pightling, Petronella and Pagotto, 2014).

Isolates from the serovar Enteritidis PT14b outbreak which clustered together when analysed with cgMLST were highly congruent with clusters obtained by SNP analysis. All clusters contained identical sets of isolates; however, there were some differences between the cgMLST and SNP analyses when more distant relationships among the clusters were examined. The differences between the approaches are likely due to the differences between the data points the two approaches analyse. This demonstrates that cgMLST provides a standardised approach, which is capable of high resolution and reliable isolate characterisation, even though the accessory genome and intergenic regions are not included. The cgMLST approach also does not exclude analysis with SNP-based approaches, if required.

The cgMLST types can be visualised with a variety of tools widely available on the internet, a number of which have been incorporated into the EnteroBase website. As the two principal features of this outbreak were date and location of isolation, these were used for diagram annotation. The cgMLST analyses supported the conclusions established by the SNP analyses that there is no relationship between country of isolation and the genetic spread of the isolates and that the diversity within the outbreak was generated at the source (Dallman *et al.*, 2016). Additionally, data presented by Inns *et al*. (Inns *et al.*, 2015) demonstrated that cases occurred concurrently across the UK over the outbreak period, further supporting this conclusion.

The clustering of isolates by cgMLST type suggested that there was a relationship between the date of isolation and the spread of the cgMLST types. The most prevalent

cgMLST types varied over the course of the outbreak, as dominant strains were replaced at approximately monthly intervals. This observation was further supported by the epidemiological data (Inns *et al.*, 2015), which showed several 'peaks' in incidence across the outbreak, at least in part caused by point-source outbreaks (Dallman *et al.*, 2016), and a decreasing 'tail' of cases at the end of the outbreak. Throughout the outbreak period, multiple strains were in continual circulation, as several cgMLST types which occurred at the start of the outbreak initially declined in prevalence but later reoccurred.

Restaurants and vendors were found to be contaminated with genotypes that clustered together when analysed with cgMLST; however, there was no known relationship between them, such as the wholesalers who supplied them (Inns *et al.*, 2015). Conversely, one wholesaler supplied to multiple restaurants and vendors but the cgMLST types associated with these businesses did not cluster together in the phylogenetic analyses. Each time a restaurant or vendor was contaminated, it was with the same cgMLST type, suggesting that these locations were only contaminated once and from a single source. These conclusions are consistent with of the epidemiological data (Inns *et al.*, 2015; Dallman *et al.*, 2016; Chatt *et al.*, 2017) and demonstrate that cgMLST can be used to make epidemiologically relevant inferences.

When isolates are closely related, they will also have parts of the accessory genome in common with each other. This can be captured by a wgMLST analysis. As there is a current lack of standardisation (Maiden *et al.*, 2013), this paper uses the scheme provided by EnteroBase, which defines wgMLST as a reference free analysis. In this

wgMLST scheme all shared genes of the given dataset are compared. Although this analysis is potentially capable of providing more resolution among isolates than cgMLST, by containing more loci, a wgMLST scheme is likely to contain pseudogenes and paralogous genes due to the inclusion of all shared genes within a dataset. The inclusion of pseudogenes and paralogous genes in such comparisons can generate spurious differences potentially leading to the inaccurate clustering of isolates in the analysis. Pseudogenes resemble functional genes but have lost at least some functionality, whereas duplicated genes are copies of functional genes. As such, they are often subject to different evolutionary constraints and may acquire mutations faster (Li, Stoeckert and Roos, 2003; Kuo and Ochman, 2010), which can lead to the appearance of greater divergence and misleading local relationships (Li, Stoeckert and Roos, 2003). Such differences may explain some of the inconsistencies among the cgMSLT and wgMLST schemes as the wgMLST scheme used here contained more pseudogenes and paralogous genes than the cgMLST scheme. This could be responsible for differences in the analyses described here, where the isolates from restaurants D, E, I and vendor L were observed to be more closely related to those from restaurants B,C, F and G with cgMLST (Figure 3a), while the same group of isolates was more closely related to the isolates from restaurants A, H and vendor K by wgMLST (Figure 3b). The clustering of the isolates does not always relate to important genealogical changes and variations between the two approaches may be caused by stochastic changes, within highly variable regions, which do not relate to disease or fitness (Zhou *et al.*, 2013). For these reasons a scheme that includes every possible gene in a dataset is not useful for surveillance purposes.

The cgMLST scheme was very effective in relating the outbreak isolates to the known diversity of *S. enterica* serovar Enteritidis. Using cgMLST it was possible to place the outbreak within the context of all known Enteritidis genomes that were available within EnteroBase. It is also possible to examine isolates based on other criteria, such as country or year of origin, enabling the investigation of trends and relationships that may otherwise not be immediately apparent and to identify closely related non-outbreak isolates within the database. This enables epidemiological inferences and investigations to be made, such as establishing the length of time for which a given genotype persists. For example, an outbreak of serovar Enteritidis phage type 8, linked to feeder mice was detected by PHE, through routine SNP analysis of whole genome sequences (De Pinna, 2016). Due to the low levels of isolates which were continually being fed into the population, this outbreak would not have been detected without routine data surveillance (De Pinna, 2016). The widespread adoption of the cgMLST approach will enable the identification of such relationships at the global level and over time.

One improvement of the *Salmonella* cgMLST scheme would be the implementation of a formal, standardised clustering system, to enable the sorting of cgMLST profiles into closely related groups, such as clonal complex. This is necessary for enabling the easy communication of an outbreak between laboratories, as cgMLST types are too discriminatory. One way to do this would be to adopt a similar approach to that used by PHE with SNP typing (Ashton *et al.*, 2015) and create 'cgMLST addresses' which are based on single linkage clustering to form a hierarchy of relatedness (Ashton *et al.*, 2015).

3.5 Conclusions

This work demonstrates that the cgMLST scheme presented has sufficient resolution to detect a multi-country disease outbreak caused by very closely related strains of serovar Enteritidis, and to identify sub-structure within the isolates obtained during the outbreak. The cgMLST analyses were congruent with the wgMLST analyses and previously used SNP analyses, but the cgMLST scheme has the advantage of being readily and consistently applied in different laboratories and jurisdictions as it uses a consistent set of conserved loci and allele designations. The analyses can be undertaken with more or fewer isolates making analyses performed with cgMLST both replicable and forwards and backward compatible. As the core genome is common to all members of the species, it is possible to rapidly locate outbreak isolates in the context of the known diversity of serovar Enteritidis. Finally, the availability of web-based analyses platforms enables these high-resolution analyses to be conducted with minimal requirements for locally installed bioinformatics infrastructure.

Statement of Authorship for joint/multi-authored papers for PGR thesis

To appear at the end of each thesis chapter submitted as an article/paper

The statement shall describe the candidate's and co-authors' independent research contributions in the thesis publications. For each publication there should exist a complete statement that is to be filled out and signed by the candidate and supervisor **(only required where there isn't already a statement of contribution within the paper itself).**

Title of Paper	**Comparative analysis of core genome MLST and SNP typing within a European Salmonella serovar Enteritidis outbreak**
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Student Confirmation

Student Name: Madison Pearce		
Contributions to Paper: Performed all analysis, data interpretation, prepared manuscript for publication, constructed the majority of the figures and edited all of them		
Signature	Date	

Supervisor Confirmation

By signing the Statement of Authorship, you are certifying that the candidate made a substantial contribution to the publication, and that the description described above is accurate.

Supervisor name and title:		
Supervisor comments:		
Signature	Date	

Chapter Four

A proposed core genome scheme for analyses of the *Salmonella* genus

Abstract

The salmonellae are found in a wide range of animal hosts and many food products for human consumption. All of *S. enterica* subspecies (I-VI) and *S. bongori* are capable of causing human disease, with most cases caused by subspecies I. The other *S. enterica* subspecies (II-VI) and *S. bongori* are opportunistic pathogens, predominantly affecting vulnerable individuals. Close contact with reptilian pets or wild species also increases the risk of human infection by non-subspecies I *Salmonella*. A core genome scheme has been proposed (EBcgMLSTv2.0) but not examined for analyses of isolates from across the genus *Salmonella*. Here, 252 loci were identified from the EBcgMLSTv2.0 scheme that were not present in over 2% of genomes and more than 5 genomes within *S. bongori* or any of the *S. enterica* subspecies. The removal of these loci from the EBcgMLSTv2.0 scheme resulted in a core genus scheme (SalmcgMLSTv1.0). SalmcgMLSTv1.0 clustered isolates from the same subspecies more rapidly and more accurately grouped isolates from different subspecies when compared with EBcgMLSTv2.0. In *S. enterica* subspecies I, all loci within the EBcgMLSTv2.0 scheme were present in over 98% of the isolates and this scheme should continue to be used for subspecies I analyses, while the SalmcgMLSTv1.0 scheme was more appropriate for cross genus investigations. The development of a modular system of core genome schemes would allow users to create schemes specific to their individual needs.

4.1 Introduction

The salmonellae are gram-negative gammaproteobacteria belonging to the family Enterobacteriaceae (Ewing, 1986). It is estimated that globally *Salmonella* species are responsible for 93.8 million cases of gastroenteritis, 80.3 million of which are foodborne, and 155,000 deaths (Majowicz *et al.*, 2010). Non-typhoidal *Salmonella* are responsible for an estimated yearly loss of 4.07 million DALYs, which is the highest burden of all foodborne infections (Kirk *et al.*, 2015).

The *Salmonella* genus is comprised of two species *Salmonella enterica (S. enterica*) and (*S. bongori*) (Prokaryotes, 2005; Tindall *et al.*, 2005). *S. enterica* is further comprised of six subspecies I (enterica), II (salamae), IIIa (arizonae), IIIb (diarizonae), IV (houtenae) and VI (indica) (Prokaryotes, 2005; Tindall *et al.*, 2005). The subspecies were originally determined through differences in phenotypic traits and have since been confirmed as distinct groupings through DDH (Crosa *et al.*, 1973), which has been regarded as the 'gold-standard' in genotypic species identification (Richter and Rosselló-Móra, 2009). Microbiologically, bacterial species and subspecies have been identified through morphological and biochemical traits (Parker, Tindall and Garrity, 2015); however, novel subspecies of *Salmonella* have previously been proposed, such as subspecies VII (Boyd *et al.*, 1996). This was initially identified through MLEE (Boyd *et al.*, 1996) and was also confirmed as a distinct cluster using genetic approaches (McQuiston *et al.*, 2008). A further three novel subspecies (novel subspecies A, B and C) have been proposed as a result of core genome SNPs analysis (Alikhan *et al.*, 2018).

The salmonellae can be found in a wide range of hosts (Lamas *et al.*, 2018), including mammals (Flockhart *et al.*, 2017), birds (Mellor *et al.*, 2010), reptiles (Whiley, Gardner and Ross, 2017), fish (Nguyen *et al.*, 2016) and crustaceans (Nguyen *et al.*, 2016). *S. enterica* subspecies I is primarily associated with warm-blooded animals and the non-subspecies I *Salmonella* are typically associated with cold-blooded animals (Lamas *et al.*, 2018); however, all of the subspecies and *S. bongori* have been isolated from both warm (Zottola *et al.*, 2013) and cold-blooded animals (Geue and Löschner, 2002). Non-subspecies I isolates have been found in high proportions, from animal products for human consumption, including poultry (Mellor *et al.*, 2010), cattle (Rodriguez *et al.*, 2006), sheep (Sörén *et al.*, 2015), pork (Rodriguez *et al.*, 2006) and fresh produce (Rodriguez *et al.*, 2006). They have also been found in wild animals, including birds of prey (Millan *et al.*, 2004) and wild boar (Zottola *et al.*, 2013). Additionally, subspecies I has regularly been isolated from reptilian species (Whiley, Gardner and Ross, 2017).

While non-subspecies I *Salmonella* are found in products for human consumption and the environment, they rarely cause human disease (Boore *et al.*, 2015). This is because non-subspecies I *Salmonella* are opportunistic pathogens of humans (Lamas *et al.*, 2018), with most cases affecting vulnerable individuals (Nair *et al.*, 2014; Lee *et al.*, 2016); however, in some circumstances these infections have led to complications (Mukai, Agatsuma and Ideura, 2018) and death (Mahajan *et al.*, 2003). In countries where people live in close proximity with reptiles the likelihood of *Salmonella* non-subspecies I infection increased. For example, in French Guiana, subspecies IV was responsible for 9.1% of cases compared with 0.3% in metropolitan France (Gay *et al.*, 2014). Furthermore, non-subspecies I isolates were regularly identified in reptilian pets (Whiley, Gardner and Ross, 2017), reptilian meat for consumption (Magnino *et al.*,

2009) and some ‘traditional medicines’ (Kraus, Guerra-Bautista and Alarcón-Segovia, 1991). These organisms have also been known, on rare occasions, to cause outbreaks in otherwise healthy individuals (Lowther *et al.*, 2011; Gunal and Erdem, 2014), however most *Salmonella* infections were caused by subspecies I (Boore *et al.*, 2015).

Foodborne diseases, including *Salmonella*, are monitored by the global surveillance network, PulseNet International (Swaminathan *et al.*, 2006). At the time of writing PulseNet International has identified cgMLST as the surveillance system to replace pulsed-field gel electrophoresis (Nadon *et al.*, 2017). Core genome schemes have several advantages, they can be maintained and shared using online databases (Jolley and Maiden, 2010; Alikhan *et al.*, 2018), which makes them easily portable (Kohl *et al.*, 2014) and little to no bioinformatic expertise is required by the end user (Nadon *et al.*, 2017). Additionally, these schemes are comprised of a fixed set of loci, which are reference free (Bratcher *et al.*, 2014), stable (Bratcher *et al.*, 2014; Moura *et al.*, 2017) and forward and backward compatible (Moran-Gilad *et al.*, 2015).

A cgMLST scheme for *Salmonella* has been developed for Enterobase (EBcgMLSTv2.0) (Alikhan *et al.*, 2018). Loci were chosen for inclusion within EBcgMLSTv2.0 if they were present in over 98% of the test genomes, if the coding frames were intact in over 94% and if the number of alleles was not exceptionally different from expected (Alikhan *et al.*, 2018). This ‘relaxed’ approach to a core genome definition allows for rare variants that are missing a locus which would otherwise be considered core (van Tonder *et al.*, 2014) and the imperfect nature of

draft genomes (Bratcher *et al.*, 2014), as well as permitting the removal of elements which are not experiencing direct selection pressures, including repetitive genes and pseudogenes (Moura *et al.*, 2017). EBcgMLSTv2.0 has been demonstrated to accurately characterise subspecies I outbreaks (Chapter Three) and was found to be comparable with SNP-based methods (Chapter Three), which are currently used within PHE for both routine surveillance and outbreak investigations (Ashton *et al.*, 2016). The EBcgMLSTv2.0 scheme has not, however, been systematically assessed for its performance at the genus level.

Here, over 2,000 *Salmonella* isolates, representing *S. bongori*, and *S. enterica* subspecies I, II, IIIa, IIIb, IV, VI and suggested subspecies VII, Novel A, B and C were examined using EBcgMLSTv2.0. The aim of this study was to determine if EBcgMLSTv2.0 could be used for future analyses that included isolates of *Salmonella* from multiple species or subspecies and if necessary, to create a sub-scheme of the EBcgMLSTv2.0 loci capable of performing this function. EBcgMLSTv2.0 was analysed by how accurately isolates from within the same subspecies clustered and then by how accurately the relationships between the subspecies were represented. These results determined the need for a genus cgMLST scheme (SalmcgMLSTv1.0), which was created and compared with EBcgMLSTv2.0.

4.2 Materials and Methods

4.2.1 Dataset creation and curation

Non-subspecies I isolates

A total of 1275 non-subspecies I isolates were identified with the Enterobase (Alikhan *et al.*, 2018) database (13/11/2017) from the metadata provided on deposition. Public Heath England (PHE) provided a further 235 non-subspecies I isolates that were not available in Enterobase (13/11/2017), many of which had underrepresented or novel antigenic formulae. These isolates were assembled using the SPAdes (Bankevich *et al.*, 2012) based assembly pipeline incorporated into Enterobase. A final search of Enterobase was conducted (06/03/2018) and identified a further 34 non-subspecies I isolates, creating an initial dataset of 1,544. If an isolate did not cluster phylogenetically with the subspecies specified by its metadata and it was not available for reanalysis it was removed, leaving 1480 isolates in this analysis.

Novel Subspecies

The subspecies VII, novel A, B and C are regularly misidentified due to a lack of formal recognition (Grimont and Weill, 2007). Preliminary cgMLST analyses using GrapeTree (Zhou *et al.*, 2018) showed that the majority of isolates belonging to the same subspecies, but not different subspecies, clustered when they had fewer or equal to 2750 allelic differences when using the EBcgMLSTv2.0 scheme (Alikhan *et al.*, 2018). Enterobase was interrogated for previously unidentified isolates which belonged to these novel groups, subspecies VII, novel A, B and C. This search identified a further 14 subspecies VII isolates (Enterobase metadata provided by the depositor: 1 subspecies I, 4 subspecies IV and 9 with none), a further 42 novel B isolates (Enterobase metadata provided by depositor: 3 subspecies II and 39 with none), a

further 12 novel C isolates (Enterobase metadata provided by depositor: 11 subspecies II and 1 with none) and no further novel A isolates were identified. Based on these findings the isolates with no metadata and those previously identified as subspecies I were added to analysis (50 isolates) and the metadata for all these isolates were altered for this analysis, increasing the dataset to 1530 non-subspecies I isolates (Appendix D).

Subspecies I isolates

Due to the overrepresentation of subspecies I a representative subspecies I dataset needed to be generated. Initially, the metadata for subspecies I isolates from PubMLST (Jolley and Maiden, 2010) were downloaded from the database (14,327 on 13/05/2018). These metadata were filtered to ensure that only isolates sequenced within Enterobase (Alikhan *et al.*, 2018) were included (3,071) so a consistent assembly method was used. All genomes in the data were filtered by rST (Jolley *et al.*, 2012) to remove any duplicates (2,424) and two isolates, or one where only one was available, were chosen from each serovar. For serovar Newport four isolates were chosen, representing lineages II and III (Sangal *et al.*, 2010), as these lineages have been shown to be physiologically distinct and are easily distinguished with phylogenetic approaches (Sangal *et al.*, 2010); no lineage I Newport isolates were available. The chosen isolates were then cross-referenced against Enterobase (Alikhan *et al.*, 2018) records and isolates were removed if they had mismatching subspecies or didn't cluster with subspecies I using GrapeTree (Zhou *et al.*, 2018) (Appendix E). This left a dataset of 556 subspecies I isolates, from 359 subspecies I serovars, to be used in conjunction with the 1530 non-subspecies I isolates (Appendix D).

4.2.2 Enterobase Core Genome Scheme (EBcgMLSTv2.0)

EBcgMLSTv2.0 was used as a starting point for the development of SalmcgMLSTv1.0 as loci had already undergone rigorous filtering and were required to meet strict criteria to be included within this scheme. EBcgMLSTv2.0 is comprised of 3002 loci and has been proposed as a typing scheme for the *Salmonella* genus (Alikhan *et al.*, 2018). EBcgMLSTv2.0 compiled coding sequences from 167 complete *Salmonella* genomes, 82 NCTC genomes which had been sequenced with the PacBio technology (Eid *et al.*, 2009) and one representative for each of the 288 eBurst groups based on rMLST, which encompassed the diversity of the *Salmonella* genus (Chapter Three). The coding sequences identified were grouped into gene clusters and paralogous genes were identified and removed (Chapter Three). Representative of each of the 3,258 *Salmonella* rSTs (up to May 2016) were then typed using this scheme (Chapter Three). A locus from this scheme was considered core within the *Salmonella* genus if it met three criteria: (i) if it was present in over 98% of the genomes, (ii), if the coding frames were intact in over 94% of the genomes and (iii) if the number of alleles was not significantly different from other loci (Alikhan *et al.*, 2018).

4.2.3 Genus Core Scheme Creation (SalmcgMLSTv1.0)

The genome comparator tool, developed for the $BIGS_{DB}$ (Jolley and Maiden, 2010) and hosted by pubMLST, was used to create SalmcgMLSTv1.0. The genome comparator tool compares all selected isolates using a predefined scheme, such as an rMLST or cgMLST scheme. Users can modify the minimum percentage identity required to generate a partial match, the minimum percent alignment required to align for partial match and the BLASTN word size that is required to match exactly to initiate an extension. The default values of these parameters are 70%, 50% and 20

respectively. Genome comparator generates an output of all the loci within a defined scheme, where defined allele numbers mark known alleles and missing and incomplete alleles are reported with an ‘X’ and an ‘I’ character respectively.

For the generation of SalmcgMLSTv1.0, 55 isolates were removed from the dataset as they represented duplicate EBcgMLSTv2.0 (Alikhan *et al.*, 2018) cgSTs, to ensure that no duplicate isolates were included in the analysis and that greater representation of a cgST did not lead to the removal of loci due to its absence in only that cgST.

EBcgMLSTv2.0 (Alikhan *et al.*, 2018) was used as an initial starting point for the development of SalmcgMLSTv1.0 as each locus has been rigorously analysed and was subjected to strict criteria before it was included within the scheme (Alikhan *et al.*, 2018). The cgSTs of the isolates were split into their respective subspecies, consisting of 556 subspecies I, 266 subspecies II, 303 subspecies IIIa, 424 subspecies IIIb, 318 subspecies IV, 27 subspecies VI, 18 subspecies VII, 42 subspecies novel B, 19 novel C and 54 *S. bongori.* Then their EBcgMLSTv2.0 genome profiles were analysed using the BIGSdb genome comparator tool with default parameters. A locus was removed from EBcgMLSTv2.0 if it was missing in over 2% of the isolates and over 5 isolates per subspecies. The removal of loci missing in over 2% of isolates was chosen as it matched the 98% inclusion criteria chosen for EBcgMLSTv2.0. The locus also needed to be missing in over 5 isolates, due to the small numbers of some isolates within the subspecies groups, this allowed for the creation of an accurate but conservative genus scheme. As a locus needed to be present in over 5 isolates per subspecies, novel subspecies A was removed from this analysis. The number of genes which needed to

be removed from the EBcgMLSTv2.0 (Alikhan *et al.*, 2018) per subspecies were analysed, as was the average number of genes missing per isolate per subspecies and the range of missing loci per subspecies. Graphs were produced using RStudio (RStudio Team, 2015).

4.2.4 GrapeTreeAnalysis

GrapeTree (Zhou *et al.*, 2018) has a minimum spanning tree algorithm that is capable of reconstructing genetic relationships, even with high levels of missing data (Zhou *et al.*, 2018) and was used to compare EBcgMLSTv2.0 (Alikhan *et al.*, 2018) with SalmcgMLSTv1.0, using all of the subspecies isolates (556 subspecies I, 278 II, 308 IIIa, 442 IIIb, 326 IV, 28 IV, 22 VII, 3 novel A, 48 novel B, 19 novel C and 56 *S. bongori*) (Appendix D). Minimum spanning trees were generated using both EBcgMLSTv2.0 (Alikhan *et al.*, 2018) and SalmcgMLSTv1.0 and the nodes were labelled with the respective subspecies. The branches were collapsed until nodes which represented different subspecies merged, to examine which of the subspecies were most closely related. This was repeated until all subspecies merged into a single node.

4.2.5 STRUCTURE Analysis

The STRUCTURE (Pritchard, Stephens and Donnelly, 2000; Hubisz *et al.*, 2009) algorithm has previously demonstrated the accurate inference of population structure in comparison with phylogenetic results (Pritchard, Stephens and Donnelly, 2000). It does this through identifying populations within the provided dataset and then assigning individuals to their most similar populations. In order to assign individuals to populations the algorithm analyses the distribution of different variants within their

profiles, which are used to create genetic clusters. Similar variation patterns are grouped iteratively using Bayesian algorithms. Isolates are initially assigned to random groups and then reassigned based on their variation patterns and frequencies, using a MCMC estimation (Pritchard, Stephens and Donnelly, 2000) process.

STRUCTURE analyses were performed on a subset of 73 isolates, 7 representatives of each of the included subspecies, except novel subspecies A which only had 3 representatives available. All the non-subspecies I isolates were chosen at random, ensuring there were no duplicate core genome profiles. Whereas subspecies I isolates were chosen for diversity, with two isolates randomly chosen from clade B (Falush *et al.*, 2006a) and Typhi/Paratyphi A (Falush *et al.*, 2006a; Didelot *et al.*, 2011) and three isolates chosen from clade A (Falush *et al.*, 2006a), two of these represented the serovars responsible for the most disease globally – serovars Typhimurium and Enteritidis and one was chosen at random. The STRUCTURE algorithm was run with a burn-in of 100,000 and an MCMC of 200,000 and the maximum number of populations (K) assumed was increased from the initial number of subspecies (11), until lower order taxonomical groups or no further populations were observed. Outputs from the analyses were edited using the DISTRUCT tool (Rosenberg, 2004).

The STRUCTURE analysis was performed with the alleles frequencies independent model, as the subspecies represent genetically diverse and distinct populations (Alikhan *et al.*, 2018). Both EBcgMLSTv2.0 and SalmcgMLSTv1.0 were analysed, in order to determine if there were any differences between the two schemes. The EBcgMLSTv2.0 analysis was based on 2991/3002 core genes as 11 were removed

due to the presence of paralogs in some of the isolates at these loci (Appendix F). While the SalmcgMLSTv1.0 analysis was based on 2732/2741 core genes as 9 were removed due to the presence of paralogs (Appendix F).

4.3 Results

4.3.1 *Salmonella* Genus Core Genome Scheme (SalmcgMLSTv1.0)

A locus was removed from EBcgMLSTv2.0 (Alikhan *et al.*, 2018) for the genus scheme if it was missing in over 2% of genomes and more than 5 genomes within *S. bongori* or any of the *S. enterica* subspecies, (as detailed in the materials and methods section) in order to create an accurate but conservative genus scheme. No locus had to be removed from the subspecies I analysis, as all loci were present in over 98.2% of isolates. For non-subspecies I isolates, between 10 and 108 loci were removed per subspecies (Figure 4.1a). The average number of missing loci per isolate varied widely, from 1.5 loci missing on average within subspecies I to 102.6 within *S. bongori* (Figure 4.1b). Due to some loci meeting the deletion criteria in multiple subspecies (Appendix G), a total of 252 loci were removed from EBcgMLSTv2.0 to create SalmcgMLSTv1.0. The overall variation of isolates within a subspecies also differed, as subspecies IIIb, IV, novel B, novel C and VII isolates all had a smaller range of missing loci per isolate than those of subspecies I and all had less than 1% of the EBcgMLSTv2.0 loci missing on average. In comparison subspecies IIIa, VI and *S. bongori* isolates all had a larger range of loci missing and had more than 1% of the EBcgMLSTv2.0 loci missing on average. Subspecies II isolates showed a greater range but had less than 1% of the EBcgMLSTv2.0 loci missing on average, suggesting a large diversity and variability of isolates within subspecies II isolates (Table 4.1).

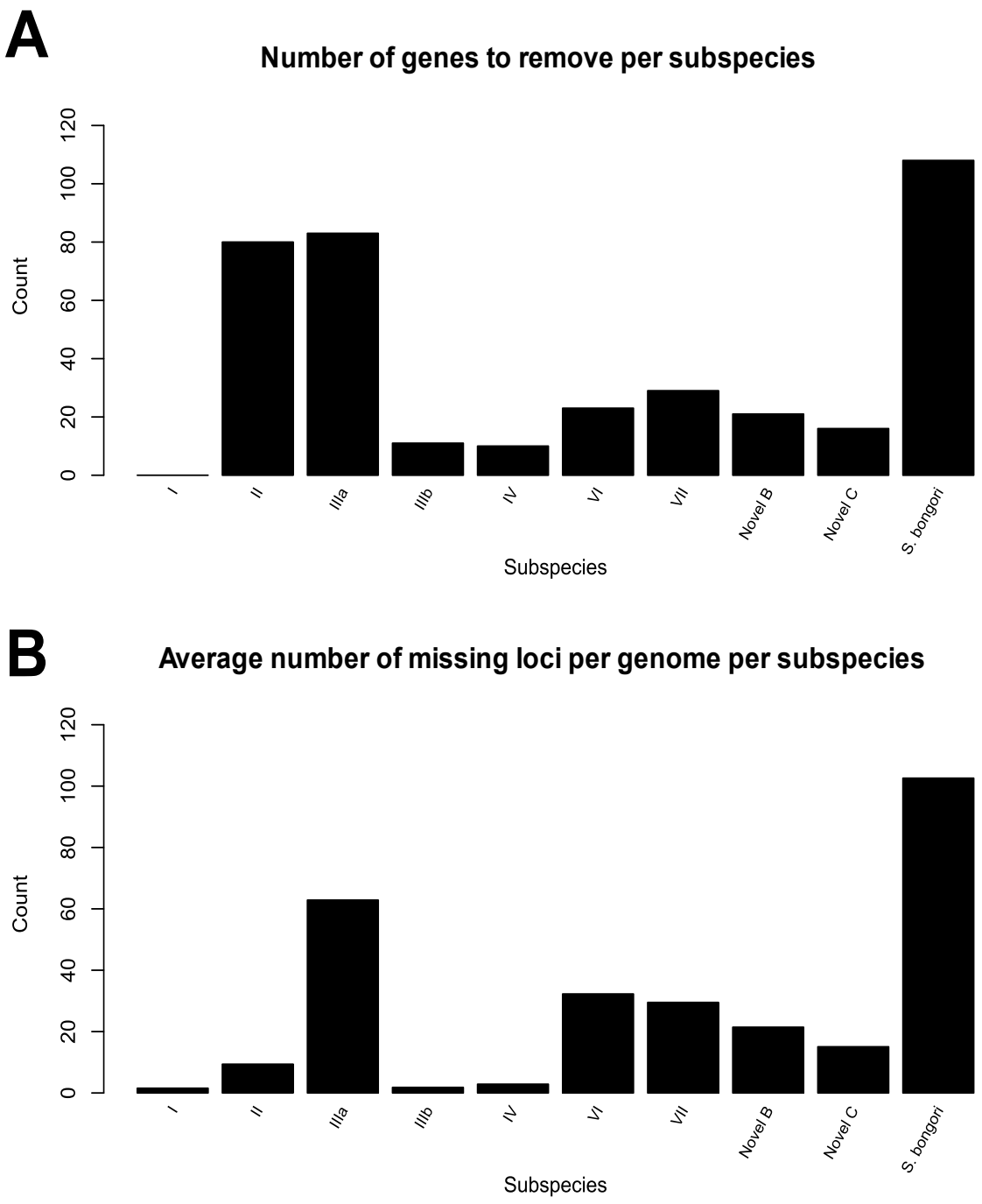


Figure 4.1: Graphs showing the number of genes to be removed per subspecies (A) and the average number of missing genes per genome per subspecies (B). Graphs showing the spread of the missing genes across the subspecies over 559 subspecies I isolates, 266 subspecies II, 303 subspecies IIIa, 424 subspecies IIIb, 318 subspecies IV, 27 subspecies VI, 18 subspecies VII, 42 subspecies novel B, 19 novel C and 54 *S. bongori*

A: The number of genes to be removed per subspecies. This graph shows that the number of genes which need to be removed from EBcgMLSTv2.0 were highly variable across the genus. EBcgMLSTv2.0 was accurate for subspecies I with no genes missing in over 2% of the genomes analysed, however the rest of the subspecies had genes which need to be removed in order to create an accurate genus scheme. *S. bongori*, subspecies IIIa and II all had over 50 genes which were missing in at least 2% of the genomes analysed.

B: The average number of missing genes per genome per subspecies. This graph shows that there is variability amongst the subspecies of the average number of missing genes per genomes. Both *S. bongori* and subspecies IIIa had a high number of missing genes per genome, while subspecies I, IIIb and IV had much lower levels of missing genes, suggesting that EBcgMLSTv2.0 was more accurate for these subspecies.

subspecies	Number of genomes in analysis	Number of loci deleted	Average number of missing loci in cg per isolate	Average percent of cg loci missing per isolate	Range of missing cg loci per isolate
I	557	0	1.54	0.05%	0 - 96
II	266	80	9.38	0.31%	0 - 213
IIIa	303	83	62.85	2.09%	51 - 264
IIIb	424	11	1.81	0.06%	0 - 67
IV	318	10	2.86	0.10%	1 - 52
Novel Subspecies B	42	21	21.43	0.71%	21 - 31
Novel Subspecies C	19	16	15.05	0.50%	11 - 30
S. bongori	*55*	108	102.58	3.42%	80 - 202
VI	27	23	32.26	1.07%	19 - 271
VII	18	29	29.5	0.98%	29 - 32

Table 4.1: Table showing the spread of missing loci per subspecies. This table shows that there is a general correlation between the average number of missing loci per isolate per subspecies and the number of loci which were not present in 98% of the genomes analysed. The main exception to this observation was subspecies II, which showed a relatively low average number of missing loci but had 80 loci meet the criteria for removal, suggesting that

there was a significant amount of diversity within subspecies II. The results also showed that there was a considerable spread amongst the subspecies in the range of missing loci per isolate with some having a range of just 3, while others had over 200, suggesting that some of the subspecies were more conserved than others.

4.3.2 GrapeTree Analysis

The overall topologies of the two minimum spanning trees were congruent, despite the removal of the 252 loci to create SalmcgMLSTv1.0 (Figure 4.2). The relative number of differences that needed to be collapsed for all isolates of the same subspecies to form a single node and the order in which nodes for subspecies merged together was changed. SalmcgMLSTv1.0 grouped almost all isolates of the same subspecies into single nodes relatively more quickly (2585/2750 loci collapsed) than EBcgMLSTv2.0 (Alikhan *et al.*, 2018) (2857/3002 loci collapsed). All subspecies I isolates and most subspecies II isolates were members of a single node consisting of isolates from their own subspecies using SalmcgMLSTv1.0 when two other subspecies had merged, conversely many subspecies I and II isolates were still separate using EBcgMLSTv2.0. Using the EBcgMLSTv2.0 the first nodes to merge were *S. bongori* and subspecies IIIa, when branches were collapsed to 2,798 differences (Figure 4.2a). This was unexpected because all *S. enterica* subspecies share a more recent common ancestor with each other than they share with *S. bongori* (Boyd *et al.*, 1996; McQuiston *et al.*, 2008; Alikhan *et al.*, 2018). It is likely to have occurred because *S. bongori* and IIIa had the most and second most missing genes respectively, therefore there were fewer loci in which they could differ. The next two nodes to merge using EBcgMLSTv2.0 were subspecies novel A and IV at 2,804 differences, which was consistent with expectations as these subspecies have been previously described as being closely

related phylogenetically (Alikhan *et al.*, 2018). In comparison, the first nodes to merge using SalmcgMLSTv1.0 were subspecies novel A and IV at 2,585 differences (Figure 4.2b) which fits with previous phylogenetic observations (Alikhan *et al.*, 2018). The next nodes to merge were subspecies VII with the IV/novel A group at 2,640 differences and again this fits with previous phylogenies of these organisms, showing that these three subspecies are closely related (Alikhan *et al.*, 2018).

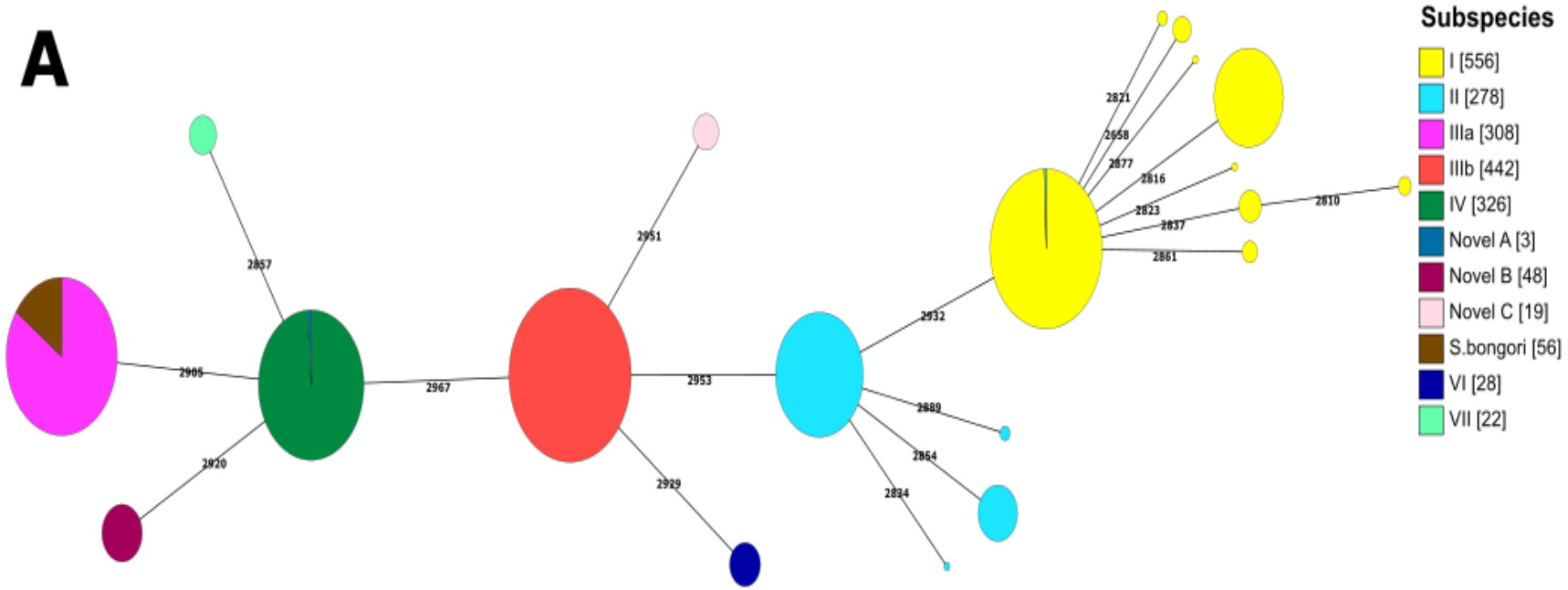


Figure 4.2: EBcgMLSTv2.0 minimum spanning tree (A) and genus core genome minimum spanning tree (B). Minimum spanning trees created with 2086 isolates, consisting of 556 subspecies I, 278 II, 308 IIIa, 442 IIIb, 326 IV, 28 VI, 22 VII, 3 novel A, 48 novel B, 19 novel C and 56 *S. bongori* were constructed via the GrapeTree (Zhou *et al.*, 2018) programme. The nodes were then collapsed until two subspecies had merged with nodes representative of another subspecies.

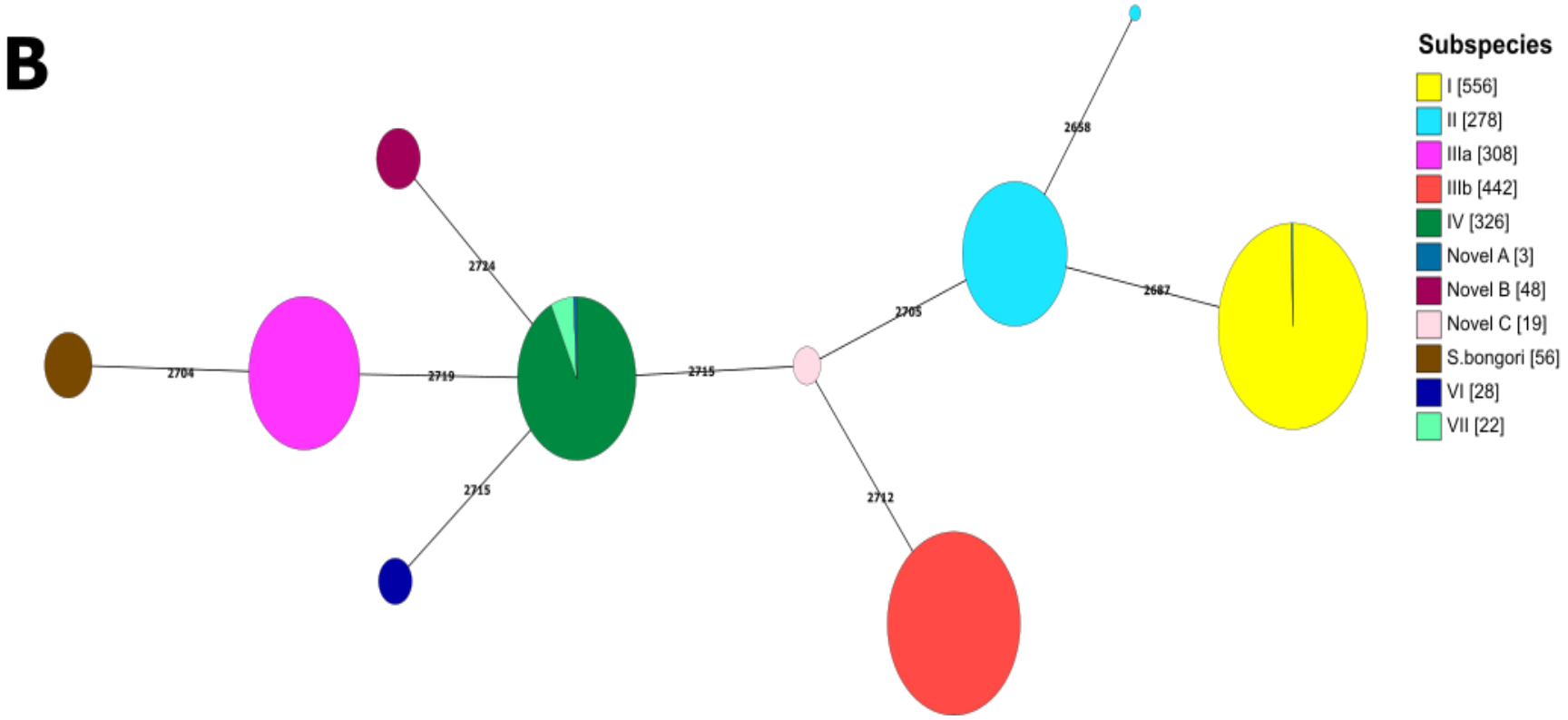


Figure 4.2: EBcgMLSTv2.0 minimum spanning tree (A) and genus core genome minimum spanning tree (B). Minimum spanning trees created with 2086 isolates, consisting of 556 subspecies I, 278 II, 308 IIIa, 442 IIIb, 326 IV, 28 VI, 22 VII, 3 novel A, 48 novel B, 19 novel C and 56 *S. bongori* were constructed via the GrapeTree (Zhou *et al.*, 2018) programme. The nodes were then collapsed until two subspecies had merged with nodes representative of another subspecies.

A: EBcgMLSTv2.0 minimum spanning tree at 2,804/3,002 nodes collapsed. The first subspecies to merge were *S. bongori* and subspecies IIIa at 2,798/3,002 nodes collapsed, followed by novel subspecies A and subspecies IV. The initial merging of *S. bongori* and IIIa indicated that EBcgMLSTv2.0 wasn't completely accurate with the biology of the *Salmonella* genus.

B: SalmcgMLSTv1.0 minimum spanning tree at 2,640/2,750 nodes collapsed. The first subspecies to merge were novel subspecies A and subspecies IV at 2,585/2,750 nodes collapsed, followed by subspecies VII merging with the subspecies IV, novel subspecies A complex. This merging was expected by the biology of the *Salmonella* genus, which shows that these 3 subspecies are amongst the closest related. This suggested that the removal of the 252 loci created a scheme which was more biologically accurate when performing analyses at the genus level.

4.3.3 STRUCTURE Analysis

The ability of the STRUCTURE (Pritchard, Stephens and Donnelly, 2000; Hubisz *et al.*, 2009) algorithm to identify the *S. enterica* subspecies and *S. bongori* differed between the two core genome schemes (Figure 4.3). When a STRUCTURE analysis was performed, with a K of 11, on EBcgMLSTv2.0 the algorithm was incapable of identifying all of the *S. enterica* subspecies, particularly subspecies IV and VI and subspecies VII and novel A. (Figure 4.3a). Analysing SalmcgMLSTv1.0, under the same parameters, the algorithm identified all of the subspecies and *S. bongori* as distinct populations (Figure 4.3b).

STRUCTURE only identified 9 of the 11 subspecies at a K of 11 when performed on EBcgMLSTv2.0 (Figure 4.3a). Subspecies II, IIIa, IIIb, novel B, novel C and *S. bongori* were all identified as distinct populations. Subspecies IV and VI isolates were indistinguishable by the programme, as were subspecies VII and 2 of the novel A isolates. EBcgMLSTv2.0 also found appreciable admixture within subspecies I serovar Oranienburg and the other novel A isolate, which could be due to recombination between these isolates, although recombination between subspecies is rare it has been previously demonstrated (Falush *et al.*, 2006a). STRUCTURE also identified the subspecies I serovars Typhi and Paratyphi A isolates as predominantly distinct populations, with a small level of admixture with the other subspecies I isolates, when EBcgMLSTv2.0 was used. The STRUCTURE algorithm resolved all of the *S. enterica* subspecies and *S. bongori* using EBcgMLSTv2.0; however, it required a larger number of populations (K = 17) and led to a higher level of admixture within subspecies I (Appendix H). Similar population structures and levels of admixture within the populations are also observed using the genus scheme with a higher number of populations (K = 16).

When STRUCTURE analysis was performed using SalmcgMLSTv1.0 the 73 isolates analysed clustered into their respective subspecies without admixture, except for the subspecies I serovar Oranienburg isolate and one of the novel subspecies A isolates (SAL_JA5200AA) (Figure 4.3b). Similarly to EBcgMLSTv2.0, the subspecies I serovar Oranienburg isolate displayed considerable admixture between subspecies I and novel subspecies A, again this is most likely due to recombination (Achtman *et al.*, 2012). The novel subspecies A isolate showed minor admixture with subspecies IV,

this is most likely due to a shared ancestry, as these subspecies are closely related (Alikhan *et al.*, 2018).

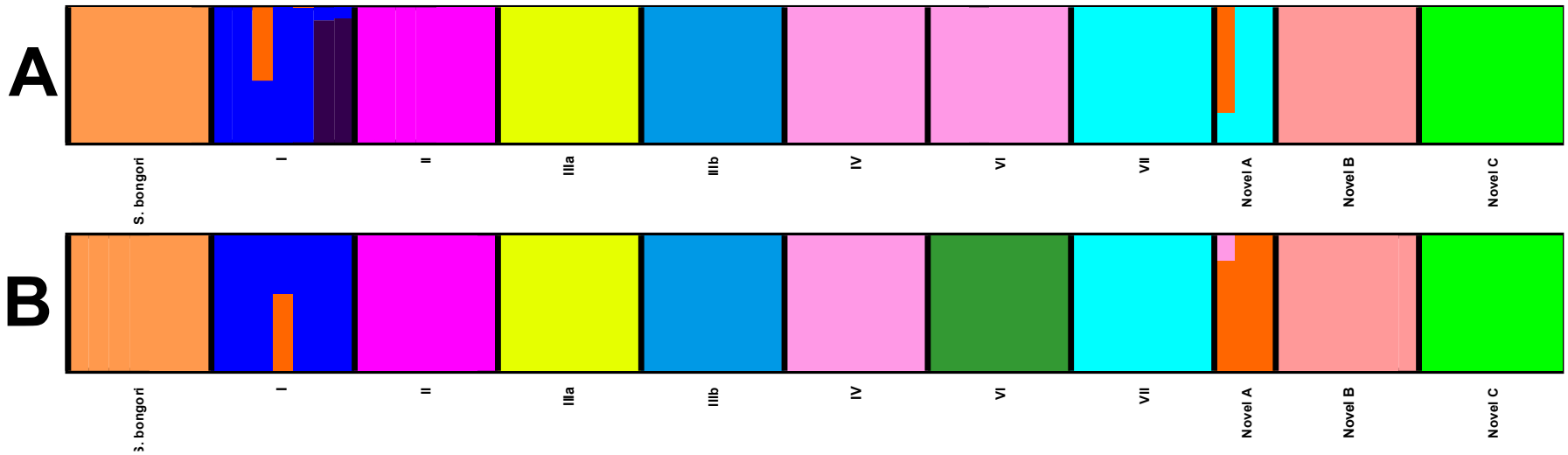


Figure 4.3: STRUCTURE analysis of 11 populations using EBcgMLSTv2.0 (A) and STRUCTURE analysis of genus core genome scheme (B). STRUCTURE (Pritchard, Stephens and Donnelly, 2000; Hubisz *et al.*, 2009) plots of 73 isolates: 7 subspecies I, II, IIIa, IIIb, IV, VI, VII, novel B, novel C and *S. bongori* and 3 novel A isolates, edited using the DISTRUCT tool (Rosenberg, 2004). These plots were created with a burn-in of 100,000, an MCMC of 200,000 and a K of 11 and compared EBcgMLSTv2.0 with SalmcgMLSTv1.0.

A: Plot showing that at a K of 11 the STRUCTURE (Pritchard, Stephens and Donnelly, 2000; Hubisz *et al.*, 2009) algorithm is incapable of identifying all the *S. enterica* subspecies and *S. bongori* when using EBcgMLSTv2.0. The algorithm finds greater statistical differences among isolates from subspecies I than it finds between subspecies IV and VI and subspecies VII and 2 of the 3 novel A isolates. This results in subspecies IV and VI forming a single population and subspecies VII and 2 of the 3 novel A isolates forming another. The subspecies I serovars Typhi and Paratyphi A are identified as a separate population with very minor admixture from the other subspecies I serovars. Subspecies I serovar Oranienburg is identified as admixed between subspecies I and the novel A isolate, this could be due to the recombinant nature of subspecies I isolates from clade B, such as Oranienburg.

B: Plot showing that at a K of 11 the STRUCTURE (Pritchard, Stephens and Donnelly, 2000; Hubisz *et al.*, 2009) algorithm identified all the *S. enterica* subspecies and *S. bongori* as distinct populations when using SalmcgMLSTv1.0. All of the isolates are highly related to other isolates from their own subspecies, with very little admixture. The largest exception was the subspecies I serovar Oranienburg isolate, which was admixed between subspecies I and novel A isolates, this is possibly due to recombination as subspecies I isolates belonging to clade B are quite variable. One isolate within subspecies novel A also showed a small degree of admixture with subspecies IV, this is most likely due to a shared ancestry between these subspecies, as they are closely related.

4.3.4 Availability of the SalmcgMLSTv1.0 scheme

This is scheme is available through PubMLST at https://pubmlst.org/salmonella and can be used for analyses on isolates within that database.

4.4 Discussion

By removing 252 loci that were missing in over 2% of isolates and more than 5 isolates in any of the subspecies or *S. bongori* from the EBcgMLSTv2.0 (Alikhan *et al.*, 2018) scheme, a *Salmonella* genus core genome scheme was generated (SalmcgMLSTv1.0) (available at pubmlst.org/salmonella). This equated to the removal of 8.39% of the EBcgMLSTv2.0 scheme. The removal of these loci was undertaken because all loci within a scheme should be present within all genomes analysed by that scheme to enable direct comparisons (Pightling, Petronella and Pagotto, 2014). These loci were originally included because EBcgMLSTv2.0 used a representative genome for each of the 3,258 rSTs which were available in the Enterobase database at the time (Chapter Three). As subspecies I is isolated and sequenced more often than all of the other species and subspecies combined (Majowicz *et al.*, 2010), most of these rSTs would have belonged to subspecies I. Consequently, the other subspecies and *S. bongori* did not constitute a large enough proportion of isolates for loci that are frequently missing within one or more of these subspecies or *S. bongori* to be removed. This was supported by the results presented here, which demonstrated that all loci were present in at least 98% of subspecies I isolates tested. The creation of the SalmcgMLSTv1.0 scheme from the EBcgMLSTv2.0 scheme allowed for compatibility between the schemes, as the loci were defined and identified using the same approaches. Compatibility between the schemes enabled easy comparison and communication of the loci.

The 252 loci were not uniformly missing from the other subspecies and *S. bongori*. Fewer than 30 loci met the criteria for removal within subspecies IIIb, IV, VII, novel B

and novel C, which equated to them missing fewer than 1% of the EBcgMLSTv2.0 loci. The other subspecies II, IIIa and VI and *S. bongori* had 80 or more loci that met the criteria for removal. Within these subspecies over 2.5% of the EBcgMLSTv2.0 loci were missing and *S. bongori* genomes were on average missing over 3.5% of the EBcgMLSTv2.0 loci. This suggests that these loci were never present or have since been lost within these subspecies and should be removed when analysing the *Salmonella* genus as a whole.

While both schemes were capable of identifying and clustering all of the subspecies and *S. bongori*, the removal of these 252 loci led to isolates from the same subspecies and *S. bongori* forming single node groups more quickly when the SalmcgMLSTv1.0 loci were analysed with GrapeTree than the EBcgMLSTv2.0 loci. This is demonstrated as using SalmcgMLSTv1.0 all subspecies I isolates and the majority of subspecies II isolates had formed single nodes at the point when two other subspecies had merged, conversely many subspecies I and II isolates were still separate using EBcgMLSTv2.0. This is most likely because the removed loci were driving the diversity within subspecies I and II, which were the final two subspecies to form single subspecies nodes when analysed using both schemes. Using EBcgMLSTv2.0 the first nodes to merge belonged to *S. bongori* and subspecies IIIa, which did not fit with previous findings that the *S. enterica* subspecies share a common ancestor (McQuiston *et al.*, 2008; Desai *et al.*, 2013). *S. bongori* and subspecies IIIa most likely merged first because they had the most and second most missing loci respectively and therefore their overall diversity was reduced as there were fewer loci in which they could differ. The considerable number of loci missing from subspecies IIIa when compared with the other *S. enterica* subspecies suggests that it could be a separate *Salmonella*

species and not a member of the *S. enterica* sepces. Further work would, however, be needed in order to confirm this observation.

In comparison, the first subspecies to merge using SalmcgMLSTv1.0 were subspecies novel A, IV and VII, which fits with previous phylogenies of these organisms that showed these subspecies were closely related (Alikhan *et al.*, 2018). While these results do not alter the capability of the schemes to detect and cluster isolates of the same subspecies with each other, they are important for exploring the relationships between species and subspecies.

Missing genes can create problems within the construction of phylogenetic trees, as they reduce the power of programs to resolve relationships (Roure, Baurain and Philippe, 2013). Increased proportions of missing genes can reduce the resolution and increase the number of stochastic errors when using maximum likelihood, Bayesian inference and maximum parsimony approaches (Lemmon *et al.*, 2009; Roure, Baurain and Philippe, 2013). It has been demonstrated that a greater level of missing data can lead to a larger long branch attraction effect, with faster evolving organisms becoming increasingly attracted to the outgroup (Roure, Baurain and Philippe, 2013). Furthermore, including genes that were missing in some organisms within an analysis reduced the ability of these approaches to detect multiple substitutions within a single position, while complete removal of a gene had only stochastic effects on the length of the branch (Roure, Baurain and Philippe, 2013). These errors, which are introduced because of missing data, highlight the need for a genus core genome scheme to

contain as few loci that are consistently missing in one or more species or subspecies as possible.

The absent genes also created problems when a subset of the subspecies and *S. bongori* were analysed using a statistical approach – the STRUCTURE (Pritchard, Stephens and Donnelly, 2000; Hubisz *et al.*, 2009) algorithm. While both core schemes were capable of identifying all of the subspecies and *S. bongori* the SalmcgMLSTv1.0 scheme was more efficient for resolving the subspecies into individual clusters and did so with less admixture. STRUCTURE identified all of the 11 subspecies when applied to the isolates typed using SalmcgMLSTv1.0 when applied to a population size of 11. In comparison, the 11 subspecies were not identified within the same isolates typed using EBcgMLSTv2.0 until the algorithm was applied to a population size of 16. When EBcgMLSTv2.0 was analysed with a population size of 11 it initially identified subspecies IV and VI, and subspecies VII and 2 of the novel A isolates as belonging to the same populations. This is because when the isolates were analysed using EBcgMLSTv2.0 STRUCTURE identified subspecies I serovars Typhi and Paratyphi A and subspecies I serovar Oranienburg and one isolate from subspecies novel A as distinct populations, over the other subspecies. It is possible that this was observed because while the diversity of all subspecies is increased by the 252 loci that were removed to create SalmcgMLSTv1.0, it has a greater effect on subspecies I, as these loci are more frequently missing within the other subspecies and *S. bongori.* Therefore, the differences created between subspecies I and *S. bongori* and the other subspecies within these 252 loci mean the algorithm falsely identified the clades (Falush *et al.*, 2006a; Didelot *et al.*, 2011) of subspecies I (Falush *et al.*, 2006b) as distinct populations before identifying all of the subspecies.

When performing analyses using the cgMLST approach the scheme should be designed for the collection of isolates being analysed, which need to be a phylogenetically coherent group. For example, human campylobacteriosis is caused by *Campylobacter jejuni* and *C. coli*, therefore for surveillance and outbreak detection a cgMLST scheme that included only these species was developed (Cody *et al.*, 2017). Whereas within *Neissiera*, a genus core scheme has been created to explore phylogenetic clustering and genetic exchange among species (Bennett *et al.*, 2010), while a scheme has also been created for *Neisseria meningitidis* (Bratcher *et al.*, 2014) for species specific investigations. This hierarchical approach has been proposed to ensure that the biological question asked and the relatedness of the organisms analysed determine the scheme to be used (Maiden *et al.*, 2013). Different cgMLST schemes can be used depending on the relatedness of the organisms, as subspecies specific schemes will have higher resolution, while species and genus schemes allow for comparisons from wider groups of organisms such as genera or families. The scheme developed here was generated to facilitate efficient and effective analyses of isolates from across the genus. It was also demonstrated that EBcgMLSTv2.0 was accurate for subspecies I, as all loci were present in at least 98% of isolates. Furthermore, previous work demonstrated that EBcgMLSTv2.0 was capable of analysing and comparing outbreak isolates within a multi-country subspecies I serovar Enteritidis outbreak (Chapter Three). As the vast majority of outbreaks are caused by subspecies I isolates EBcgMLSTv2.0 should continue to be used for outbreak analysis, as it is capable of perofrming subspecies I outbreak analyses and the increased number of loci provides increased resolution for analysis. The SalmcgMLSTv1.0 scheme should be used for the comparison of isolates from across the *Salmonella* genus.

These results provide a starting point for the creation of such a hierarchical system, where the core genome scheme used fits the isolates being analysed. A modular system of subspecies and species-specific schemes will enable users to create custom schemes, based on the particular investigation they are performing. EBcgMLSTv2.0 (Alikhan *et al.*, 2018) is a functional subspecies I scheme, the removal of the 252 loci suggested here created a genus scheme (SalmcgMLSTv1.0) and a *S. enterica* scheme can easily be created by including the loci listed here that are missing specifically from *S. bongori*. The SalmcgMLSTv1.0 scheme has been made publicly available at pubmlst.org/salmonella. Further analyses are needed to create schemes specific to the other *S. enterica* subspecies and *S. bongori*, as it is likely that loci that were excluded from EBcgMLSTv2.0, due to their absence in subspecies I, are routinely present in other subspecies. These schemes could be created and implemented in such a way as to enable them to be used in conjunction, allowing the user to create custom schemes based on their own needs. For example, a subspecies IV, VII and novel A scheme could be created to further explore the shared ancestry and subsequent divergence of these three subspecies. Further examination should also be performed on *S. enterica* subspecies IIIa, in order to determine if this subspecies should be reclassified as a separate *Salmonella* species.

4.5 Conclusions

This work demonstrates that the removal of 252 genes from EBcgMLSTv2.0 (Alikhan *et al.*, 2018) creates a more efficient and accurate scheme for analyses and characterisation of isolates across the *Salmonella* genus (SalmcgMLSTv1.0). The SalmcgMLSTv1.0 scheme has been made publicly available through pubmlst.org/salmonella. The two schemes were congruent for the clustering of isolates within their own subspecies; however, SalmcgMLSTv1.0 resolved isolates into their given subspecies grouping more quickly and identified relationships among the subspecies more precisely. The analyses undertaken here also revealed new insights into the variability of the *Salmonella* subspecies, suggesting that some had a more conserved number of loci than others. All loci within the subspecies I dataset were present in over 98% of genomes, therefore EBcgMLSTv2.0 should continue to be used for subspecies I analyses and outbreak investigations, as the inclusion of these genes will give increased resolution. Finally, it is proposed that the development of a modular system for core genome analyses will be beneficial for generating schemes that are tailored to specific requirements.

Statement of Authorship for joint/multi-authored papers for PGR thesis

To appear at the end of each thesis chapter submitted as an article/paper

The statement shall describe the candidate's and co-authors' independent research contributions in the thesis publications. For each publication there should exist a complete statement that is to be filled out and signed by the candidate and supervisor **(only required where there isn't already a statement of contribution within the paper itself).**

Title of Paper	A proposed core genome scheme for analyses of the *Salmonella* genus
Publication Status	Submitted for Publication
Publication Details	M. Pearce, M. Chattaway, K. Grant and M. Maiden

Student Confirmation

Student Name: Madison Pearce		
Performed all analysis, data interpretation, prepared manuscript for publication, constructed and edited all of the figures.		
Signature	Date	

Supervisor Confirmation

By signing the Statement of Authorship, you are certifying that the candidate made a substantial contribution to the publication, and that the description described above is accurate.

Supervisor name and title:		
Supervisor comments:		
Signature	Date	

Chapter Five

An evaluation of speciation and subspeciation of the *Salmonella* genus using whole genome sequencing

Abstract

Species and subspecies within the *Salmonella* genus have been defined through their biochemical properties; however, public health reference laboratories are increasingly adopting sequence-based methods for surveillance and routine identification, leading to potential disparity between the biochemical subspecies definitions, routine typing and the ability to detect novel subspecies. Due to the routine sequencing of *Salmonella* isolates there is now sequence data available for a large number of isolates, which enabled a large-scale analysis of the *Salmonella* genus to determine subspeciation at the genetic level. This analysis demonstrated that the *Salmonella* species and subspecies were genetically distinct, including those identified through phylogenetic approaches – subspecies VII, novel A (VIII), novel B (IX) and novel C (X) and identified a novel subspecies (subspecies XI). Analysis of these genomes indicated that *S. enterica* subspecies IIIa isolates were ancestral to the other *S. enterica* subspecies and were sufficiently distinct to be classified as a separate species, *S. arizonae*. The multiple phylogenetic and statistical approaches generated congruent results, suggesting that the species structure of the *Salmonella* genus is conserved. Biochemical analyses of these species and subspecies demonstrated that not all of the subspecies were biochemically distinguishable. The disparity between the genetic and biochemical clusters demonstrated that biochemical approaches were not consistently representative of the relationships within the genus. Recommended standardised genomic definitions of species and subspecies and a genome-based routine typing approach for the identification and definition of novel subspecies are described here.

5.1 Introduction

Defining prokaryotic species has long been controversial (Konstantinidis, Ramette and Tiedje, 2006). The most widely accepted approach is for organisms to have (i) at least one consistent distinguishable phenotypic trait and (ii) at least 70% DDH (Wayne *et al.*, 1987), combining both the phenotype and genotype of isolates. Within the *Salmonella* genus isolates are classified through a range of tests that determine biochemical properties (Grimont and Weill, 2007); however, the nomenclature and taxonomy within this group has presented problems (Brenner *et al.*, 2000; McQuiston *et al.*, 2008). Some clarity was achieved in 2005 through a judicial opinion (Prokaryotes, 2005) and an accompanying commentary by Tindal et al. (Tindall *et al.*, 2005), which split the genus into two species, *Salmonella bongori (S. bongori)* (Reeves *et al.*, 1989; Prokaryotes, 2005) and *Salmonella enterica (S. enterica)* (Prokaryotes, 2005). *S. enterica* is divided into a further six subspecies (Tindall *et al.*, 2005): *Salmonella enterica* subspecies I (*enterica), Salmonella enterica* subspecies II (*salamae*), *Salmonella enterica* subspecies IIIa (*arizonae)*, *Salmonella enterica* subspecies IIIb (*diarizonae)*, *Salmonella enterica* subspecies IV (*houtenae*) and *Salmonella enterica* subspecies VI (*indica*) (Tindall *et al.*, 2005). The phenotypic distinctions among the subspecies have been further confirmed by DNA (Reeves *et al.*, 1989; Boyd *et al.*, 1996) and genetic characteristic analyses (Boyd *et al.*, 1996; McQuiston *et al.*, 2008).

A MLEE analysis (Boyd *et al.*, 1996) demonstrated the presence of a genetically distinct group – *Salmonella enterica* subspecies VII, which was confirmed using a genetic analysis (McQuiston *et al.*, 2008). Due to biochemical approaches identifying

subspecies VII as subspecies IV (Boyd *et al.*, 1996) it has not been formally recognised (Grimont and Weill, 2007). A further 3 novel subspecies have been identified using a core genome SNPs analysis (novel A, B and C) but no biochemical analysis has so far been performed on these possible subspecies for backwards compatibility (Alikhan *et al.*, 2018).

The lack of formal recognition of subspecies VII highlights the problems of a typing scheme based on biochemical characteristics (Grimont and Weill, 2007). Biochemical and microbiological subspeciation methods are incapable of accurately representing the genetic relationships among isolates (Boyd and Hartl, 1998; McQuiston *et al.*, 2008), require microbiological expertise across a wide range of biochemical tests and are low throughput (Herrera-León *et al.*, 2004). Additionally, reference laboratories, such as PHE, have started to replace biochemical approaches with genome-based approaches, which allows greater resolution of the genetic relationships among isolates (Ashton *et al.*, 2016; Crook *et al.*, 2016; Holmes *et al.*, 2018). The WGS approach of cgMLST has been adopted as the replacement for PFGE by PulseNet (Nadon *et al.*, 2017), meaning that global monitoring of foodborne disease will rely on this technology (Nadon *et al.*, 2017).

While this move toward WGS based typing allows for increased understanding and more accurate reporting, the majority of research, and therefore publications, have focused on subspecies I, as it has been responsible for most *Salmonella* infections in humans (CDC, 2008). However, the other subspecies have also been responsible for cases of human disease (team *et al.*, 2008), as they are opportunistic pathogens

(Lamas *et al.*, 2018) and can infect humans under certain conditions. Most reported cases have occurred within vulnerable individuals, such as the young (team *et al.*, 2008), elderly (Nair *et al.*, 2014) and immunocompromised (Hoag and Sessler, 2005). Non-subspecies I *Salmonella* have been isolated from animal sources including exotic reptilian pets (Wikström *et al.*, 2014), wild (Zottola *et al.*, 2013; Gay *et al.*, 2014) and zoo animals (Romero *et al.*, 2016), chickens (Duffy, Dykes and Fegan, 2012), livestock (Rodriguez *et al.*, 2006; Sörén *et al.*, 2015) and farmed reptiles (Madsen, 1996). The primary hosts for non-subspecies I isolates are thought to be reptiles, as isolates have been found in snake, crocodile, lizard and turtle species (Madsen, 1996; Nowakiewicz *et al.*, 2012; Wikström *et al.*, 2014). Reptile farms from across the globe, including the United Kingdom, have had non-subspecies I salmonellae isolated from them (Magnino *et al.*, 2009).

When humans are in close contact with reptiles the chances of transmission of non-subspecies I serovars increases (Gay *et al.*, 2014). In French Guiana a correlation between *Salmonella* serotypes in patients and those found in local reptile populations was found, with two-thirds of reptile serotypes also isolated from patients (Gay *et al.*, 2014). A total of 16.7% of reptiles were positive for subspecies IV, which was responsible for 10% of human salmonellosis cases. Reptiles are thought to be a natural reservoir for non-subspecies I (Schröter *et al.*, 2004; Nowakiewicz *et al.*, 2012) and it is estimated that more than 1% of households in the USA and Europe are now home to either a reptile or amphibian species (American Veterinary Medical Association, 2007; Romero *et al.*, 2016). This increase in exotic pets could lead to an increase in cases of salmonellosis from subspecies II – VI. For instance, one study examining 16 pet snakes found 13 of them were infected with subspecies IIIb (Schröter

et al., 2004) and another found subspecies II in 8 out of 80 pet turtles, most of which were infected with more than one strain (Nowakiewicz *et al.*, 2012).

The increased prevalence of reptilian and amphibian household pets and consumption of reptilian meat (Lamas *et al.*, 2018), combined with reptiles being a natural reservoir (Schröter *et al.*, 2004; Nowakiewicz *et al.*, 2012) for non-subspecies I isolates, emphasises the need for a uniformly accepted characterisation of the genus *Salmonella*. This is further highlighted by the difficulties of conventional biochemical approaches to subspeciation (Herrera-León *et al.*, 2004) within *Salmonella*. However, with reference laboratories adopting WGS (Ashton *et al.*, 2016) and increased sequencing sharing through databases (Jolley and Maiden, 2010; Alikhan *et al.*, 2018), a largescale examination of the complete *Salmonella* genus is now possible.

An analysis of isolates from across the *Salmonella* genus was undertaken here, with the aim of identifying and defining a genome-based approach to *Salmonella* speciation and subspeciation. All isolates were analysed in a search for previously unidentified novel subspecies and examinations were undertaken with both genetic and biochemical approaches. Additionally, all confirmed species and subspecies and previously identified novel subspecies (VII, novel A, B and C) were re-examined using statistical and phylogenetic approaches, in order to help confirm or deny their existence as genetically distinct clusters. Finally, a comparison of rMLST and cgMLST for subspecies identification was performed.

5.2 Materials and Methods

5.2.1 Isolate collection and curation

Collection and curation of non-subspecies I isolates

The non-subspecies I isolates used previously (Chapter Four) were used in this analysis (06/03/2018), as they had all been confirmed as non-subspecies I isolates. This resulted in a dataset of 1530 isolates containing: 278 subspecies II, 308 IIIa, 442 IIIb, 326 IV, 28 IV, 22 VII, 3 VIII, 48 IX, 19 X and 56 *S. bongori (*Appendix I) (Chapter Four). These isolates were confirmed using metadata and phylogenetic clustering or reanalysis within a reference laboratory. For all of these isolates the subspecies provided for the metadata in Enterobase by the original uploader matched with their genetic clustering, with the exception of SAL_MA5841AA (Enterobase ID), which was reanalysed at PHE via microbiological testing and was still identified as subspecies II, although it clustered with subspecies I isolates during genetic analyses (Chapter Four).

Subspecies I isolates

As subspecies I was overrepresented within databases, a representative subset was identified for analysis. This subset consisted of the twenty *S. enterica* subspecies I serovars most commonly identified by PHE within the UK. To create this dataset eBGs, based on MLST (Achtman *et al.*, 2012), were used. This approach linked identical ST and single locus variants to create groups of genetically closely related isolates (Achtman *et al.*, 2012). If a single eBG group was comprised of more than 10% of isolates from a single serovar then up to 10 representative isolates were randomly chosen from PHE isolates. If there were fewer than 10 isolates available from PHE then as many as were available were used, this created a subset of 271 subspecies I

representative isolates (Appendix I). PHE isolates were used as they were validated by a reference laboratory and it was possible to reanalyse the isolates if there were any discrepancies between phylogenetics and the metadata.

Identification of novel subspecies

The 1530 non-subspecies I isolates and the 271 subspecies I isolates were used to construct rMLST and cgMLST minimum spanning trees in GrapeTree (Zhou *et al.*, 2017), which were used to identify potential novel subspecies. A potential novel subspecies was defined as a group of three or more isolates that did not merge with any other subspecies with any other subspecies when branches in the minimum spanning trees were collapsed. Groups of three or more isolates were chosen to ensure the presence of a real subspecies and not the result of a mixed sample or a single highly mutated strain. To identify novel subspecies branches were collapsed until the nodes of two confirmed subspecies merged or multiple phylogenetically identified subspecies merged with a confirmed subspecies, creating a single node. When a new subspecies was identified, Enterobase (Alikhan *et al.*, 2018) was searched for further isolates of these novel subspecies that may have been uploaded without metadata or incorrect metadata and were therefore missed in the initial searches for non-subspecies I isolates. All novel subspecies were assigned the next available roman numeral, novel subspecies A, B and C (Alikhan *et al.*, 2018) were therefore assigned subspecies VIII, IX and X.

5.2.2 Datasets (Appendix J)

Dataset A: 569 isolates that were representative of the diversity of *Salmonella* (Tindall *et al.*, 2005; Trüper, 2005) were used to create rMLST and cgMLST NJTrees (Saitou

and Nei, 1987) and a rMLST ML phylogeny (Goldman, 1990) and for the STRUCTURE analysis of the rMLST loci. The dataset consisted of: 29 *S. bongori* isolates, 100 *S. arizonae*, 95 subspecies I, 100 subspecies II, 100 subspecies IIIb, 100 subspecies IV, 16 subspecies VI, 5 subspecies VII (Boyd *et al.*, 1996), 3 subspecies VIII, 8 subspecies IX, 10 subspecies X and 3 subspecies XI. Isolates were chosen from the 1801 isolates to represent the rSTs (Jolley *et al.*, 2012) within each species or subspecies. Up to 100 isolates, all with different rSTs, were randomly chosen or as many as were available, with the exception of subspecies XI where two isolates with the same rST were used as only three isolates were available in total.

Dataset B: 77 isolates that were used for a cgMLST STRUCTURE analysis. The 77 isolates represented seven randomly chosen examples of each suspected subspecies, except subspecies VIII and XI, which only had three available. Isolate SAL_BA7507AA (Enterobase ID) was also included in the analysis, as it clustered with different subspecies when phylogenetic trees were created using rMLST and cgMLST. The subspecies I isolates were chosen for diversity, with three random examples from clades A and B (Falush *et al.*, 2006) and two from the Typhi/Paratyphi A lineage (Falush *et al.*, 2006; Didelot *et al.*, 2011) (one Typhi and one Paratyphi A).

Dataset C: 25 isolates were selected for ANI comparisons. For the confirmed subspecies, type strains from the Judicial Commission of the International Committee on Systematics of Prokaryotes (Trüper, 2005) were used for between species and subspecies comparisons. This included one *S. bongori*, two *S. arizonae*, three *S. enterica* subspecies I, two subspecies II, two subspecies IIIb, two subspecies IV and

one subspecies VI isolates which had previously been defined as type strains and deposited in the NCTC culture collection. One subspecies VII, one subspecies VIII, two subspecies IX, two subspecies X and one subspecies XI were proposed as type strains. The remaining one subspecies VI and one subspecies VII were from PHE and the remaining one subspecies VIII and one subspecies XI were chosen at random from the remaining isolates (any Enterobase isolates), as there were only represented by three genomes. Three type strain isolates were selected for subspecies I, one isolate each from clades A and B (Falush *et al.*, 2006) and one from the Typhi/Paratyphi A lineage (Falush *et al.*, 2006; Didelot *et al.*, 2011), enabling an average to be taken for within subspecies I comparisons.

Dataset D: 25 isolates were randomly chosen for an ANI analysis. Two isolates of *S. bongori*, *S. arizonae*, subspecies II, IIIb, IV, VI, VII, VIII, IX, X and XI were selected at random. Three isolates of subspecies I were selected, one representative each from clades A and B (Falush *et al.*, 2006) and one from the Paratyphi A/Typhi (Falush *et al.*, 2006; Didelot *et al.*, 2011) lineage.

Dataset E: 22 representative genomes were selected from the PHE archives for a phenotypic analysis of all of the species and subspecies. Two isolates were used for *S. bongori, S. arizonae,* subspecies I, II, IIIb, IV, VI, IX and X, one isolate was used for subspecies VII, VIII and XI as only one example of these subspecies were available within PHE archives. Isolate SAL_MA5841AA that grouped phylogenetically with subspecies I but was typed as subspecies II using microbiological approaches was also included for further analysis.

5.2.3 Phylogenetic analyses

The rMLST alleles of the isolates in dataset A (Appendix J) were used to generate a phylogeny using the Neighbour joining algorithm (Saitou and Nei, 1987). The NJtree (Saitou and Nei, 1987) was generated using the Genome Comparator tool (Jolley and Maiden, 2010) from the BIGS$_{DB}$ (Jolley and Maiden, 2010) provided by PubMLST. The tree was rooted using the *S. bongori* species as an outgroup and annotations were performed using the ITOL online tool (Letunic and Bork, 2016).

For comparison the dataset A isolates (Appendix J) were also used to construct a NJtree (Saitou and Nei, 1987) using the GenuscgMLSTv1.0 scheme (Chapter Four). The NJtree (Saitou and Nei, 1987) was generated using the Genome Comparator tool from BIGS$_{DB}$ (Jolley and Maiden, 2010). This tree was also rooted using *S. bongori* as an outgroup and annotations were performed using the ITOL online tool (Letunic and Bork, 2016).

In order to confirm the accuracy of the NJtree (Saitou and Nei, 1987) the rMLST sequences were used to reconstruct a ML phylogeny (Goldman, 1990). The rMLST sequences of dataset A (Appendix J) were exported from BIGS$_{DB}$ (Jolley and Maiden, 2010) after being aligned using MAFFT (Katoh *et al.*, 2002). The ML tree (Goldman, 1990) was constructed using MEGA7 (Kumar, Stecher and Tamura, 2016) with 100 bootstrap replications calculated using the Kimura 2-parameter model (Kimura, 1980). The tree was rooted using the *S. bongori* species as an outgroup and annotations were performed using the ITOL online tool (Letunic and Bork, 2016).

5.2.4 Statistical analyses

STRUCTURE: The STRUCTURE (Pritchard, Stephens and Donnelly, 2000; Hubisz et al., 2009) algorithm has been shown to infer population structure accurately when compared with expected phylogenetic results (Pritchard, Stephens and Donnelly, 2000). It identified populations from the given data as well as assigning an individual to the population to which it was most similar. The algorithm analysed differences in the distribution of variants within multilocus typing profiles of a dataset to create genetic clusters. Individuals that share similar variations patterns are grouped by a Bayesian iterative algorithm. STRUCTURE applied MCMC estimations, which initially assigned individuals to a random group and then reassigned them based on estimations on variant frequency (Pritchard, Stephens and Donnelly, 2000).

STRUCTURE (Pritchard, Stephens and Donnelly, 2000) was applied to both rMLST (Jolley *et al.*, 2012) and cgMLST (Alikhan *et al.*, 2018) data, using the allele frequencies independent model, as the subspecies represented genetically diverse and distinct populations (Boyd *et al.*, 1996; Alikhan *et al.*, 2018). For both analyses the maximum number of populations assumed (K) was increased from 12 until no further populations were observed and until lower order taxonomical groups were observed, such as the splitting of subspecies I into its respective clades (Falush *et al.*, 2006; Didelot *et al.*, 2011).

The rMLST analysis was performed on dataset A (Appendix J). In the rMLST analysis, results were based on 51/53 ribosomal genes as BACT000060 (*rpmE*) and BACT000065 (*rpmJ*), were excluded as they were paralogous genes present in the

genome. The rMLST analysis was run with a burn-in of 100,000 and 150,000 MCMC repetitions. The output was edited and annotated using the DISTRUCT (Rosenberg, 2004) software.

The cgMLST analysis was based on 2746/2750 core genes, as 4 were removed (STMMW_36391, STMMW_00801, STMMW_44771 and STMMW_05221) from the analysis due to the presence of paralogs in more than three of the genomes analysed, if a locus was paralogous in 2 or fewer genomes then the paralogous loci were replaced with the value for a missing locus. The cgMLST analysis was conducted on dataset B (Appendix J), with a burn-in of 100,000 and 200,000 MCMC repetitions.

ANI: For the ANI (Konstantinidis, Ramette and Tiedje, 2006) calculations an online ANI calculator that used the OrthoANIu (Lee *et al.*, 2016) algorithm was used. This algorithm was chosen because the ANI scores between two genomes can vary when reciprocal calculations are compared (Lee *et al.*, 2016). In comparison OrthoANI fragmented both genomic sequences and only used the orthologous pairs to calculate the nucleotide identities. OrthoANI was highly comparable with traditional ANI but the values were approximately 0.1% higher (Lee *et al.*, 2016).

The ANI was calculated by comparing the WGS of isolates from dataset C (Appendix J). Pairs of isolates with ANI values higher than 95% (Klappenbach *et al.*, 2007; Richter and Rosselló-Móra, 2009) were considered to be from the same species. ANI analyses to identify species with the 95% criteria were performed on the entire genome sequence and not on a subset of genes such as wgMLST. As there was no percentage

cut-off for subspecies, this comparison was used to identify the difference in values within and between the subspecies. The analysis was repeated using the same genomes at the levels of cgMLST and rMLST. Analysis of the WGS of randomly selected subspecies representatives were also performed to confirm the results obtained using the type strains.

For comparison with the results from the type strain analysis, ANI values were also calculated from randomly chosen isolates (dataset D [Appendix J]) to confirm the results observed within that analysis.

OrthoANI was used to analyse isolates SAL_MA5841AA and SAL_BA7507AA against dataset C and dataset D isolates, as these isolates had conflicting results within previous analyses. SAL_MA5841AA clustered with subspecies I isolates when analysed using all of the phylogenetic approaches and the STRUCTURE analysis of the rMLST loci, however it was identified as subspecies II using phenotypic approaches. SAL_BA7507AA clustered with subspecies II isolates when a NJTree was constructed using cgMLST loci and a STRUCTURE analysis of the rMLST loci, however when a NJTree was constructed using rMLST loci it clustered with subspecies XI and a STRUCTURE analysis of the cgMLST loci identified it as a further novel subspecies.

5.2.5 Phenotypic analyses

The phenotypic metabolic respiration of the isolates in dataset E (Appendix J), were analysed using a Biolog metabolic assay (Technopath). The *Salmonella* strains were streaked onto blood agar plates (Oxoid) and were incubated at 37°C overnight. A

single colony pick was inoculated using a flat end cotton swab into type A broth (Technopath) and mixed thoroughly. Each well of a Biolog Gen III 96 well MicroPlate, which contained metabolites or a negative control (https://biolog.com/products-portfolio-overview/microbial-identification), was inoculated using 100µl of the broth and placed into the Biolog at an incubation temperature of 33°C. The plate was read every 15 minutes for 48 hours in order to record the metabolic respiration of these isolates. Runs were repeated independently 3 times.

The results were analysed by calculating the signal value (Homann *et al.*, 2005) for each run. The signal value equalled the ([average signal over 48 hours + maximum signal over 48 hours]/2) – (the average signal over the first 2 hours) (Homann *et al.*, 2005). An average signal value for each subspecies was calculated via RStudio (RStudio Team, 2015) and used in order to create a heatmap of substrate utilisation for metabolic phenotyping and a dendrogram based on metabolic respiration values. The heatmap and dendrogram of substrate utilisation were created to assess if utilisation of biochemical properties could be used to identify all of the *Salmonella* species and subspecies.

5.3 Results

5.3.1 Assignment of *Salmonella* subspecies

No incongruencies between the metadata of subspecies I isolates and phylogenetic clustering were observed in the preliminary analyses (Appendix K), with the exception of SAL_MA5841AA, which was phenotypically identified as subspecies II but clustered with subspecies I isolates phylogenetically. Within the rMLST minimum spanning tree, constructed using GrapeTree (Zhou *et al.*, 2017) (Appendix K(a)), it was found that when branches were collapsed to 20/51 allelic differences (Appendix K(c)) then the nodes representing subspecies II and IIIb merged, whereas within the cgMLST minimum spanning tree (Appendix K(b)) at 2640 /2750 allelic differences subspecies VII and novel A (VIII) merged with subspecies IV (Appendix K(d)). Any cluster of three or more isolates that did not cluster with any other subspecies and was present in both the rMLST and cgMLST trees was identified as a potential novel subspecies. There was one cluster of subspecies II isolates which met these criteria (SAL_DA4561AA, SAL_EA2466AA and SAL_MA5907AA), these isolates were therefore identified as a novel subspecies – subspecies XI. Species *S. bongori* and *S. enterica* were identified, as were subspecies I, II, IIIa, IIIb, IV, VI, VII, VIII, IX, X and XI; however, subspecies IIIa was identified as a separate species.

5.3.2 Phylogenetic Analyses

Both the rMLST (Figure 5.1a) and cgMLST (Figure 5.1b) NJTrees (Saitou and Nei, 1987) of dataset A (Figure 5.1) showed that *S. bongori* was ancestral to all of the other isolates and that *S. arizonae* (previously *S. enterica* subspecies IIIa) was ancestral to all *S. enterica* subspecies. These trees (Figure 5.1) showed that all of the *S. enterica*

subspecies identified through traditional methods (II, IIIb, IV and VI) and those identified through phylogenetic approaches (VII [MLEE], VIII, IX, X [SNP-based MLtree] and XI [minimum spanning tree]) all formed distinct monophyletic groups. In both of the trees, subspecies IV, VII and VIII formed a clade of closely related subspecies but all of the subspecies remained monophyletic. These results were highly congruent with previously produced results (McQuiston *et al.*, 2008; Desai *et al.*, 2013; Alikhan *et al.*, 2018), demonstrating consistency within the identification of *Salmonella* subspecies, despite the use of different phylogenetic methods. The overall topologies of the two trees were highly congruent (Figure 5.1), demonstrating that rMLST was capable of discriminating between *Salmonella* isolates down to at least the subspecies level.

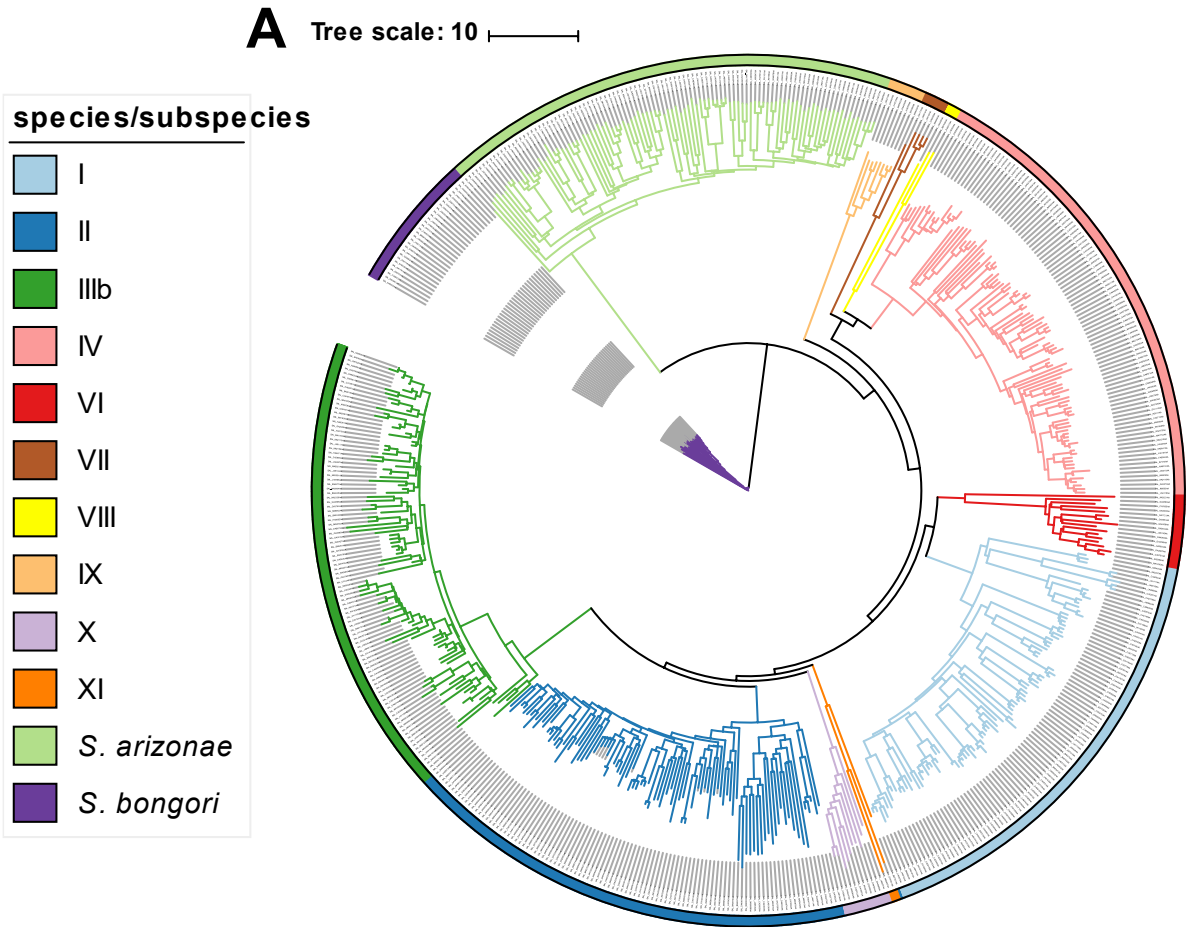


Figure 5.1: NJTree based on the rMLST loci of 569 representative isolates (A) NJTree based on the cgMLST loci of 569 representative isolates (B). Neighbour-Joining Trees of 569 isolates. Each isolate was randomly selected from the 1801 initial isolates to represent up to 100 different rST profiles per species or subspecies. The presence of distinct clades supported the findings of novel subspecies and the reclassification of subspecies IIIa to *S. arizonae*, as it was also ancestral to the other subspecies. The trees were constructed using the BIGSdb Genome Comparator tool and SplitsTree software and were edited using the ITOL online tool. Both trees were rooted using *S. bongori* and were highly congruent.

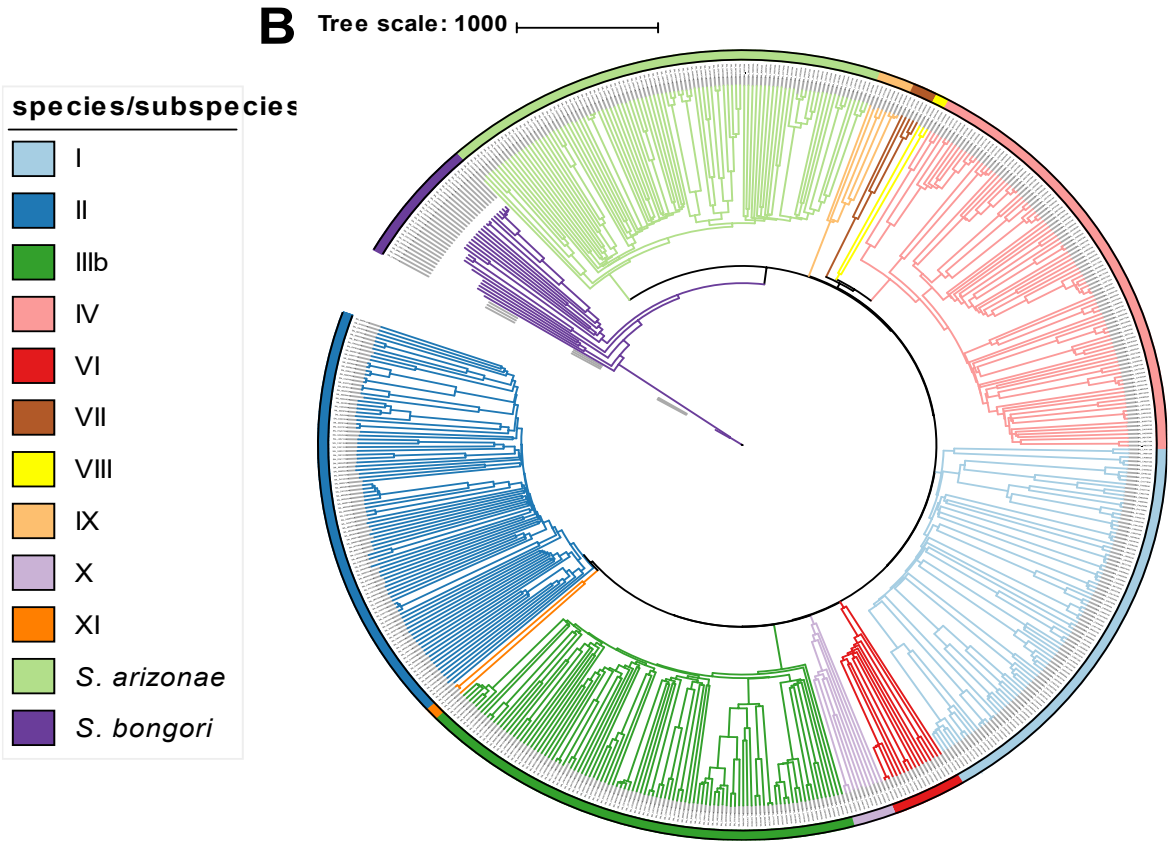


Figure 5.1: NJTree based on the rMLST loci of 569 representative isolates (A) NJTree based on the cgMLST loci of 569 representative isolates (B). Neighbour-Joining Trees of 569 isolates. Each isolate was randomly selected from the 1801 initial isolates to represent up to 100 different rST profiles per species or subspecies. The presence of distinct clades supported the findings of novel subspecies and the reclassification of subspecies IIIa to *S. arizonae*, as it was also ancestral to the other subspecies. The trees were constructed using the BIGSdb Genome Comparator tool and SplitsTree software and were edited using the ITOL online tool. Both trees were rooted using *S. bongori* and were highly congruent.

A: NJTree of 569 isolates, based on rMLST. The rMLST tree clustered all of the species and subspecies into distinct clades. The species and subspecies identified through traditional biochemical methods and those identified through phylogenetic approaches all formed distinct clades. The only isolate that didn't cluster as expected was SAL_BA7507AA, from initial phenotypic and phylogenetic investigations it clustered with subspecies II but clustered with subspecies XI using this approach.

B: NJTree of 569 isolates, based on cgMLST. All species and subspecies expect for *S. bongori* formed distinct clades. *S. bongori* was split into multiple clades, all of which were ancestral to *S. arizonae* and *S. enterica* isolates, this could be because the diversity within *S. bongori* has not been well explored and it is feasible that *S. bongori* is also comprised of multiple subspecies. Within the cgMLST tree SAL_BA7507AA clustered with subspecies II but was ancestral to the rest of the subspecies II clade, suggesting that it could be representative of another novel subspecies.

This suggested that the increased time and computational power required to generate the increased resolution of a cgMLST tree was not necessary for subspecies identification. One isolate (SAL_BA7507AA) did not cluster as expected within the rMLST tree (Figure 5.1a) based on the results of phenotypic and initial phylogenetic investigations. SAL_BA7507AA was a subspecies II isolate but within the rMLST tree it clustered with subspecies XI. Within the cgMLST tree (Figure 5.1b) SAL_BA7507AA clustered with subspecies II, however it was ancestral to the rest of the subspecies II clade. Within the cgMLST tree *S. bongori* did not form a single monophyletic clade.

In order to confirm the results observed within the NJtrees a MLtree (Goldman, 1990) was created for the rMLST profiles (Appendix L). The topologies of the NJtree and the

MLtree were also highly congruent, with *S. bongori* ancestral to all of the other isolates and *S. arizonae* ancestral to all of the *S. enterica* subspecies. Within the rMLST MLtree all of the subspecies nodes were highly supported with bootstraps of 0.89 or greater. The consistencies between the MLtree and the NJtree demonstrated that the increased resolution of the MLtree and the increased time taken in order to produce the tree provided no further insight into subspeciation and the relationships between the salmonellae and was therefore unnecessary.

5.3.3 Statistical Analyses

STRUCTURE: STRUCTURE (Pritchard, Stephens and Donnelly, 2000) analyses using both rMLST and cgMLST loci (Figure 5.2) also supported the presence of *S. bongori*, *S. arizonae* and *S. enterica* as separate species, along with the *S. enterica* subspecies I, II, IIIb, IV, VI, VII, VIII, IX, X, and XI. All of the species and subspecies formed distinct and consistent clades.

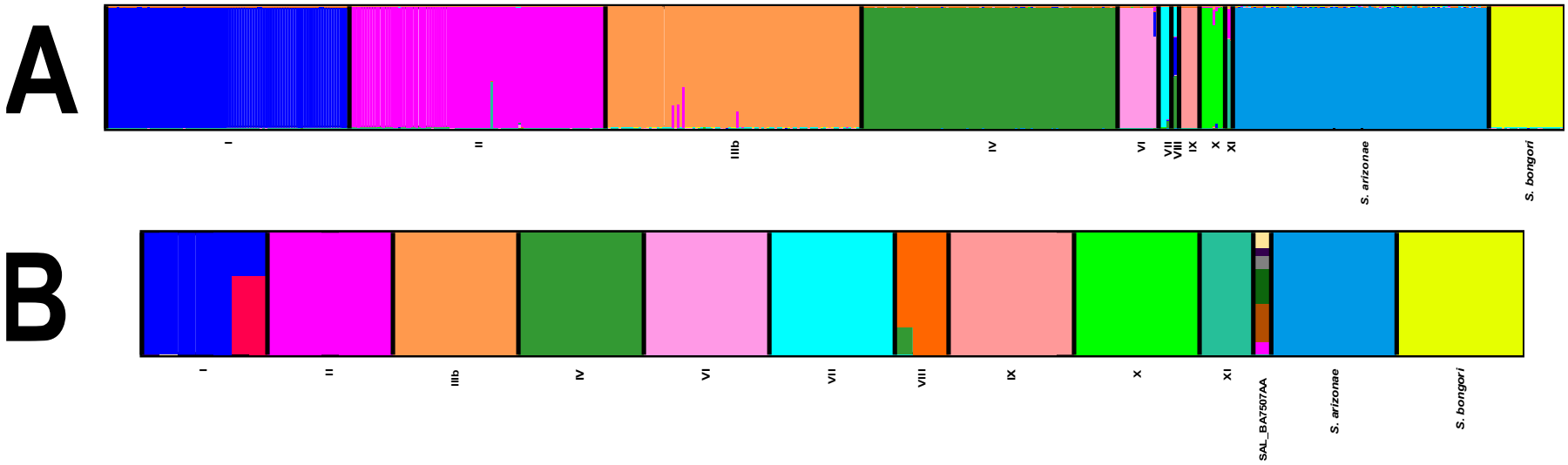


Figure 5.2: STRUCTURE **analysis (A) of 569 isolates using rMLST (B) of 57 isolates using cgMLST.** STRUCTURE analyses of representative isolates of the species and subspecies. The STRUCTURE algorithm was run until no further higher-level taxonomical groups were observed. These analyses showed that all of the subspecies formed individual clusters when analysed using the algorithm. These results also supported the identification of the novel subspecies and the reclassification of subspecies IIIa as *S. arizonae*. Both of the STRUCTURE outputs were edited using the DISTRUCT software.

A: The STRUCTURE algorithm was performed on the rMLST profiles of dataset A (Appendix J) isolates with a K of 12. All of the species and subspecies were identified as distinct clusters when using a K of 12 and no further populations were identified at a higher K. *S. bongori*, *S. arizonae* and subspecies I, II, IIIb, IV, VI, VII, IX and X showed very little admixture and were all distinct populations. In comparison subspecies VIII and XI were composed of multiple rMLST populations. Subspecies VIII was an admixture of subspecies VII, IV and I, all of which were present in similar proportions in each isolate of subspecies VIII. Subspecies XI was predominantly a novel population, however there was consistently a high level of admixture from subspecies II. The isolate SAL_BA7507AA grouped with subspecies II via the STRUCTURE analysis.

B: The STRUCTURE algorithm was performed on the cgMLST profiles of Dataset B (Appendix J) with a K of 18. At a K of 18 all of the species and subspecies were identified as distinct populations. Species *S. bongori* and *S. arizonae* and subspecies II, IIIb, IV, VI, VII, IX X and XI were all distinct population with almost no admixture. Subspecies I serovars Paratyphi A and Typhi also formed a distinct population (red), but also showed admixture with the rest of subspecies I, this is most likely due to shared ancestry between these isolates and the novel population due to the host restricted nature of these serovars and the reduction in genome size. One isolate of subspecies VIII was admixed with subspecies IV, this was most likely due to shared ancestry as these subspecies are closely related. Isolate SAL_BA7507AA was highly admixed with five novel populations and some of subspecies II, again this suggested that SAL_BA7507AA may represent a novel subspecies but further isolates and examination would be needed in order to confirm this observation.

The STRUCTURE algorithm performed on the rMLST loci of dataset A identified 12 distinct groups (Figure 5.2a). The species *S. bongori, S. arizonae and* the *S. enterica* subspecies I, II, IIIb, IV, VI, VII, VIII, IX, X and XI were all identified as distinct

populations. At a K of 12 the species *S. bongori, S. arizonae* and *S. enterica* subspecies I, II, IIIb, IV, VI, VII, IX and X were all represented by single populations that showed very little admixture. In comparison subspecies VIII and XI were comprised of multiple rMLST populations and as such showed significant admixture. *S. enterica* subspecies VIII was comprised of an admixture of subspecies I, IV and VII that were all present in similar proportions. Subspecies XI was an admixture of subspecies II and a novel population. Within the rMLST STRUCTURE analysis isolate SAL_BA7507AA clustered with the other subspecies II isolates. At an increased value of K no further populations were observed, only increased admixture between the twelve subspecies groups. The results of this STRUCTURE analysis supported the presence of the twelve species or subspecies and the phylogenies created from the same datasets.

In comparison the STRUCTURE algorithm performed on the cgMLST loci of dataset B isolates identified 13 distinct groups (Figure 5.2b). At a K of 18 STRUCTURE identified species *S. bongori, S. arizonae* and the *S. enterica* subspecies I, II, IIIb, IV, VI, VII, VIII, IX, X and XI. However, the *S. enterica* subspecies I isolates from the Typhi/Paratyphi A lineage (Falush *et al.*, 2006; Didelot *et al.*, 2011) were admixed between the subspecies I population and a distinct population (red). One isolate of subspecies VIII also demonstrated a small amount of admixture with subspecies IV. Using cgMLST isolate SAL_BA7507AA also formed a distinct population that was highly admixed and was composed of five novel populations and subspecies II. Higher values of K revealed no further subspecies, subspecies became more admixed and split into lineages.

ANI: The WGS ANI (Lee et al., 2016) performed on dataset C showed that comparisons of all of the species and subspecies against *S. bongori* scored below 90% and comparisons against *S. arizonae* scored below 95% (Figure 5.3a). All of these values were below the 95% cut-off used within ANI analyses to determine separate species (Klappenbach *et al.*, 2007; Richter and Rosselló-Móra, 2009). Comparisons between the *S. enterica* subspecies had ANI values between 92.93 – 97.13%, with an average of 95.15%. Comparisons within the subspecies were all higher, with ANI values between 97.89 – 99.99% (Figure 5.3a). These results supported the reclassification of *S. enterica* subspecies IIIa to a separate subspecies (*S. arizonae*) (Figure 5.3) and the presence of the novel subspecies identified through phylogenetic techniques (VII, VIII, IX, X and XI) (Boyd *et al.*, 1996; Alikhan *et al.*, 2018).

The ANI analyses were repeated using the cgMLST (Figure 5.3b) and rMLST loci (Figure 5.3c) and the patterns observed within these analyses were highly similar to those observed within the WGS analysis. Within the cgMLST analysis *S. bongori* and *S. arizonae* were all still lower than the 95% threshold, required for the classification of species (Klappenbach *et al.*, 2007; Richter and Rosselló-Móra, 2009), which further supported the reclassification of *S. enterica* subspecies IIIa to *S. arizonae*. Furthermore, comparisons between the *S. enterica* subspecies (94.3 – 97.71%, with an average of 96.10%) were again lower than comparisons within subspecies (98.79 – 100%). These patterns persisted down to the rMLST loci (Figure 5.3c).

The recommended type strains (Appendix M) will be submitted to the NCTC database and will be given NCTC accession numbers. These isolates will be publicly available.

A) Whole Genome Sequences

	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	S. arizonae	S. bongori
I	98.37											
II	96.15	98.3										
IIIb	95.16	96.04	99.53									
IV	95.01	95.42	95	99.49								
VI	95.62	96	95.19	94.82	99.99							
VII	93.68	93.96	93.96	96.63	93.61	99.51						
VIII	95.82	95.44	94.71	97.13	94.77	96.45	97.89					
IX	94.57	95.2	94.78	94.15	94.61	92.93	94.08	99.79				
X	95.05	95.86	95.67	94.98	95.45	93.83	94.82	94.79	99.41			
XI	95.72	97.04	96.05	95.36	95.81	94.02	95.16	95.09	95.96	98.79		
S. arizonae	93.35	93.88	93.83	93.37	93.16	93.04	93.24	92.85	93.47	93.66	99.33	
S. bongori	89.79	89.91	89.78	89.54	89.58	89.38	89.62	89.5	89.54	89.72	89.31	99.39

B) rMLST

	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	S. arizonae	S. bongori
I	99.82											
II	99.34	99.88										
IIIb	99.13	99.47	99.92									
IV	98.83	99.09	99.05	99.9								
VI	99.13	99.37	99.25	98.89	100							
VII	98.53	98.72	98.65	99.15	98.56	99.84						
VIII	99.01	99.03	98.94	99.47	98.81	99.02	99.42					
IX	98.76	98.94	98.82	98.72	98.73	98.44	98.74	99.93				
X	99.25	99.43	99.29	98.93	99.17	98.54	98.94	98.82	99.89			
XI	99.06	99.33	99.16	98.81	99.13	98.48	98.77	98.72	99.16	99.79		
S. arizonae	98.56	98.61	98.42	98.42	98.39	98.3	98.42	98.26	98.46	98.41	99.82	
S. bongori	98.2	98.4	98.34	98.07	98.36	98	98.12	98.06	98.3	98.29	98	99.95

C) cgMLST

	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	S. arizonae	S. bongori
I	98.79											
II	96.94	99.01										
IIIb	96.13	96.89	99.69									
IV	95.97	96.47	96.07	99.7								
VI	96.42	96.98	96.33	96.03	100							
VII	94.63	95.21	95.05	96.86	94.76	99.54						
VIII	96.62	96.22	95.86	97.26	95.88	96.54	98.79					
IX	95.64	96.25	95.86	95.32	95.78	94.3	95.17	99.88				
X	96.37	96.92	96.66	95.98	96.33	94.94	95.82	95.91	99.77			
XI	96.7	97.71	96.9	96.43	96.7	95.13	96.05	96.14	96.85	99.2		
S. arizonae	94.33	94.77	94.89	94.58	94.21	94.26	94.42	94.07	94.46	94.71	99.4	
S. bongori	91.1	90.89	91.11	90.8	90.7	90.53	90.73	90.94	90.97	90.91	90.33	99.54

Figure 5.3: ANI analysis of (A) type strains and recommended type strains using WGS (B) ANI analysis of type strains and recommended type strains using rMLST (C) ANI analysis of type strains and recommended type strains using cgMLSTv1.0. ANI analyses of isolates from dataset C (Appendix J). Each isolate was compared to all of the other species or subspecies isolates and with a secondary isolate that belonged to the same species or subspecies using the OrthoANI algorithm. Isolates of the same species or subspecies were always more closely related than isolates from different species or subspecies. *S. arizonae* and *S. bongori* were most distantly related to isolates from *S. enterica*, supporting their classification as different species.

A: ANI analysis of type strains and recommended type strains using WGS. Within this analysis all comparisons of species and subspecies against *S. bongori* scored below 90% similarity, which is well below the 95% cut-off for isolates belonging to the same species. Comparisons against *S. arizonae* also all scored below the 95% cut-off, although the comparisons were all higher, supporting the reclassification of subspecies IIIa as a species. Comparisons between the other subspecies all ranged between 92.93% - 97.13%, with an average of 95.15%. On the other hand, comparisons within the subspecies ranged from 97.89% - 99.99%. The differences between the subspecies support the belief that the novel subspecies identified through phylogenetic techniques are truly novel.

B: ANI analysis of type strains and recommended type strains using the rMLST loci. The patterns observed within the rMLST analysis was very similar to that observed within the cgMLST and WGS analyses. This suggested that the patterns observed within the relatedness of the species and subspecies persisted down to the rMLST loci.

C: ANI analysis of type strains and recommended type strains using cgMLST. The cgMLST analysis was congruent with the WGS ANI results. *S. bongori* and *S. arizonae* were still lower than the 95% threshold, supporting the reclassification of subspecies IIIa as a species. Comparisons between the other subspecies (94.3% - 97.71%, with an average of 96.10%) were again lower than comparisons within subspecies (98.79% - 100%).

ANI analyses on WGS, cgMLST loci and rMLST loci were repeated using randomly selected isolates for all of the species and subspecies (dataset D). The results were highly congruent between the chosen type strains and the randomly selected isolates. Using WGS and cgMLST both *S. bongori* and *S. arizonae* scored below the 95% threshold for all comparisons (Appendix N(a)). The ANI values for the comparisons of the WGS of the *S. enterica* subspecies I isolates scored between 93.14 – 97.55%, whereas comparison within subspecies had ANI values between 98.41 – 99.94%.

Using the cgMLST loci comparisons between subspecies isolates had ANI values between 94.32 – 98.11% and comparisons within subspecies all had higher ANI values ranging between 99.8% - 99.96% (Appendix N(b)). This further supported the presence of the novel subspecies (VII, VIII, IX, X and XI) and the reclassification of *S. enterica* subspecies IIIa to *S. arizonae*. The rMLST analysis was once again congruent with the WGS and the cgMLST analyses (Appendix N(c)).

The percentage rises from WGS to cgMLST to rMLST were consistent throughout the comparisons. The patterns of relatedness between the three approaches were highly consistent, suggesting that ANI was scalable across the different genomic levels.

When isolate SAL_BA7507AA (which clustered with subspecies XI in a NJTree constructed using rMLST loci and with subspecies II when the tree was constructed using cgMLST) was analysed using ANI against both dataset C and D it was closely related to subspecies II and XI, scoring 97.99% and 97.87% respectively for dataset C and 97.65% and 97.69% respectively for dataset D (Appendix O(a)). However, these values were all lower than comparisons within the subspecies II and subspecies XI isolates, which all scored above 98%. This suggested that SAL_BA7507AA could be representative of another novel subspecies or could represent a mid-point between these two subspecies.

Whereas when isolate SAL_MA5841AA (which was phenotypically typed as subspecies II but clustered with subspecies I isolates phylogenetically) was analysed against datasets C and D it was very closely related to subspecies I, scoring 99.89%

and 99.98% respectively (Appendix O(b)). This further supported SAL_MA5841AA genetically belonging to subspecies I and that the identification through biochemical methods did not accurately cluster this isolate with those to which it was most closely related.

5.3.4 Phenotypic analyses

The averages of the signal values (Homann *et al.*, 2005) from 3 independent Biolog runs (Appendix P(a, b and c)) were used to construct a dendrogram based on metabolic respiration values (Figure 5.4). The dendrogram based on metabolic respiration showed that the species *S. bongori* and *S. arizonae* (previously subspecies IIIa) were phenotypically most closely related to members of their own species.

This was also true for the conventionally identified subspecies II, IIIb, IV and VI and the phylogenetically identified subspecies XI, also formed an independent branch. The signal values clustered subspecies VII (Boyd *et al.*, 1996) and VIII (Alikhan *et al.*, 2018) with subspecies IV.

In the dendrogram subspecies I and X isolates did not cluster with each other or other subspecies (Figure 5.4). The signal values identified subspecies I serovar Enteritidis as ancestral to the subspecies IV, VII and VIII clade and serovar Typhimurium was ancestral to the *S. arizonae* clade. One of the subspecies X isolates was ancestral to the subspecies II isolates, the other clustered with isolate I/II (SAL_MA5841AA) (Figure 5.4), which biochemical approaches and the PHE Kmer approach identified as subspecies II but had clustered phylogenetically with subspecies I isolates. The

subspecies IX isolates did not form a single clade (Figure 5.4) but were both ancestral to the same clade. Prior to identification and subsequent reclassification as novel subspecies, subspecies IX, X and XI were all identified as subspecies II via metadata; however, the dendrogram produced from the signal values demonstrated that none of these subspecies were in the same clade as subspecies II (Figure 5.4). In particular, subspecies IX and XI were not closely related phenotypically to subspecies II (Figure 5.4).

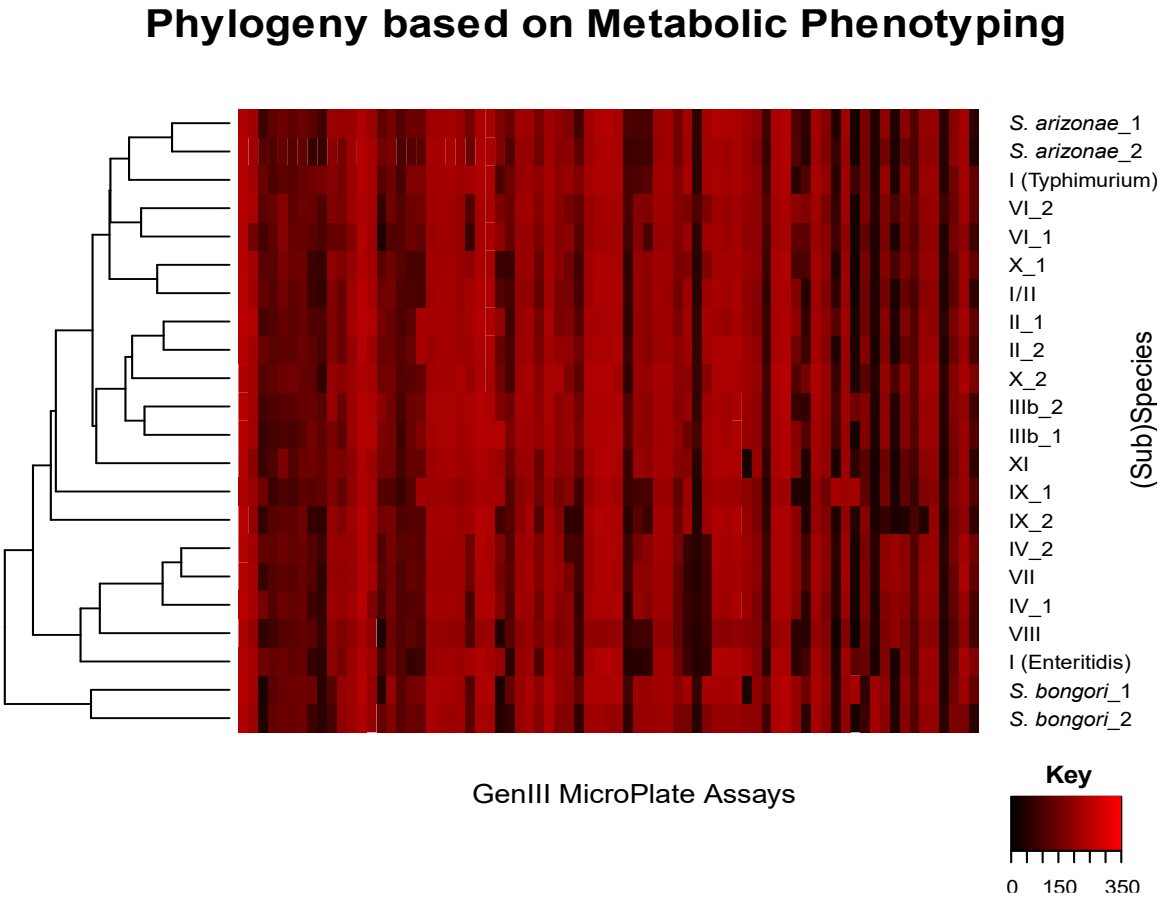


Figure 5.4: Phylogeny based on metabolic phenotyping using an average of 3 runs on the Biolog GenIII MicroPlate Assays. Species *S. arizonae and S. bongori* were more closely related to each other phenotypically than other isolates, as were *S. enterica* subspecies II, IIIb, VI and XI. Subspecies VII and VIII clustered with subspecies IV, which was expected as subspecies VII and VIII are phenotypically identified as subspecies IV and are closely related genetically as well. Subspecies X did not specifically cluster with any other subspecies or each other. Phenotypically one subspecies X isolate clustered with subspecies II, while the other clustered with the isolate which was phenotypically subspecies II but genetically subspecies I, these subspecies II groups did not cluster together. Subspecies IX did not cluster together but were both ancestral to the same clade, suggesting that they were closely related. Subspecies I isolates did not cluster together but this was probably due to these isolates being different serovars, which have different uses of the metabolites. Subspecies IX, X and XI are currently identified as subspecies II, these results fully support the reclassification of subspecies IX and XI and somewhat support the reclassification of subspecies X.

5.4 Discussion

In the genomic era, the conventional approaches for speciation and subspeciation of the genus *Salmonella* are outdated. Species and subspecies are currently defined and identified by morphological and metabolic difference, despite the uptake of WGS by reference laboratories (Ashton *et al.*, 2016; Holmes *et al.*, 2018), such as Public Health England (Ashton *et al.*, 2016; Crook *et al.*, 2016). Additionally, the global monitoring of foodborne disease outbreaks by PulseNet is changing to the genome-based method of cgMLST (Nadon *et al.*, 2017). In order to correspond with how *Salmonella* isolates are now routinely monitored (Ashton *et al.*, 2016) and analysed (Nadon *et al.*, 2017), it is necessary to change how these species and subspecies are classified and identified. The routine usage of genomes also provides a feasible solution to *Salmonella* speciation and subspeciation.

Metabolic respiration of 22 *Salmonella* isolates, representative of all of the *Salmonella* species and subspecies identified through both phenotypic and phylogenetic approaches, was examined in this study. The dendrogram produced from these metabolic respiration values demonstrated that phenotypic typing is not always capable of delineating the *Salmonella* subspecies (Figure 5.4). This was true for both phenotypically identified subspecies, such as subspecies I and for phylogenetically identified subspecies such as IX and X. The representatives for these subspecies did not form subspecies specific clades within the dendrogram of the metabolic respiration values. Isolates representative of subspecies VII and VIII, which were identified as subspecies through phylogenetic methods (Boyd *et al.*, 1996; Alikhan *et al.*, 2018), clustered with subspecies IV. The representatives of both species (*S. bongori* and *S.*

arizonae), the majority of the conventionally identified subspecies (II, IIIb, IV and VI) and some of the phylogenetically identified subspecies (IX and XI) formed distinct clades. While there were phenotypic differences between most of the subspecies, the inability for biochemical approaches to consistently distinguish all of the subspecies demonstrated the need for a shift in how subspecies are identified.

In contrast, phylogenetic methods consistently identified all of the subspecies. All of the species and subspecies formed distinct clades irrespective of the phylogenetic approach used. Trees created using the Neighbour-Joining algorithm (Saitou and Nei, 1987) based on the rMLST (Jolley *et al.*, 2012) and cgMLST (Chapter Three) loci (Figure 5.1) and a phylogeny created using the ML algorithm (Goldman, 1990) based on the rMLST loci (Appendix L) were highly congruent. *S. bongori* was the most divergent of the *Salmonella* species, this was shown by the phylogenies, as all of the *S. bongori* isolates were ancestral to all of the other isolates. Unlike in the rMLST phylogenies (Figure 5.1a, Appendix L), in the cgMLST phylogeny (Figure 5.1b) *S. bongori* did not form a single monophyletic clade. This could be due to high levels of diversity within the *S. bongori* species, as the diversity of *S. bongori* has not been well documented and it could therefore also be comprised of multiple subspecies. In all of the phylogenies (Figure 5.1, Appendix L) *S. arizonae* (previously subspecies IIIa) was also ancestral to the other *S. enterica* subspecies, indicating that it was another species and not a *S. enterica* subspecies. The *S. enterica* subspecies were highly consistent across the phylogenies, except for one isolate (SAL_BA7507AA), which clustered with subspecies XI using rMLST and subspecies II using cgMLST (Figure 5.1). These phylogenies demonstrated that the genetic differences between the subspecies were highly conserved, as the relationships between the species and

subspecies were observable when trees are constructed with the 2750 cgMLST loci or using the 51 rMLST loci (Figure 5.1).

The clades observed within the phylogenies were also highly congruent with those observed when the isolates were analysed with the STRUCTURE algorithm (Figure 5.2) (Pritchard, Stephens and Donnelly, 2000). All of the species and subspecies formed distinct populations using both rMLST and cgMLST. While the rMLST analysis identified the three species (*S. bongori, S. arizonae* and *S. enterica*) and ten *S. enterica* subspecies at a population of twelve (Figure 5.2a), the cgMLST required a population of eighteen to identify all of the species and subspecies (Figure 5.2b). In the cgMLST analysis serovars Typhi and Paratyphi A were split into their own population, which was admixed with the subspecies I population. It is likely this distinct population occurred due to the host restricted nature of these serovars (Holt *et al.*, 2009; Spanò, 2016), the reduction in their genome size (Didelot *et al.*, 2007) and recombination between the two serovars (Didelot *et al.*, 2007; Holt *et al.*, 2009). Furthermore, one isolate of subspecies VIII also demonstrated a degree of admixture with subspecies IV (Figure 5.2b), this was likely to be because these subspecies were closely related (Alikhan *et al.*, 2018). Isolate SAL_BA7507AA (Enterobase ID) was also highly admixed, being composed of five novel populations and the subspecies II population (Figure 5.2b).

The high levels of admixture observed within isolate SAL_BA7507AA and the ambiguity over whether it was more closely related to subspecies II, as was shown in the cgMLST phylogeny (Figure 5.1b) or subspecies XI, as was shown in the rMLST

phylogeny (Figure 5.1a) suggested that this isolate could also represent a novel subspecies. Analysis of isolate SAL_BA7507AA with ANI found that it was on the threshold for subspeciation with both subspecies II and XI, suggesting that while it could be representative of a novel subspecies, it could also represent an admixed sample or even a midpoint of speciation between subspecies II and XI. The results in regard to isolate SAL_BA7507AA remain ambiguous and further isolates would be needed to confirm whether this was a novel subspecies or distantly related to subspecies II or XI.

ANI (Lee *et al.*, 2016) analyses were conducted for the final confirmation of the *Salmonella* species and subspecies (Figure 5.3). Results from these analyses demonstrated that both *S. bongori* and *S. arizonae (*previously subspecies IIIa) met the criteria for designation as separate species, as comparisons with isolates from the other *Salmonella* species consistently scored below 95% average nucleotide identity (Figure 5.3a). The comparisons between the *S. enterica* subspecies were more variable, some comparisons scored below the 95% cut-off while others scored above (Figure 5.3a). However, the ANI values for between subspecies comparisons were consistently lower than those for within subspecies comparisons (Figure 5.3). This supported the classification of subspecies I – XI as separate subspecies.

The findings from the ANI analyses also supported a change from conventional biochemical methods to phylogenetic approaches, as the results from the ANI analyses were highly congruent with those observed in both the phylogenies and from the STRUCTURE analyses. Routinely isolates can be typed using sequence typing

methods, such as cgMLST (Chapter Three) (Alikhan *et al.*, 2018) or rMLST (Jolley *et al.*, 2012). The results from this study demonstrated that both rMLST and cgMLST were highly congruent and are capable of routine identification of subspecies. The cgMLST phylogeny provided no more meaningful resolution than the rMLST phylogenies, therefore rMLST should be used for routine speciation and subspeciation, as rMLST requires less computational power and curation of fewer loci (Jolley *et al.*, 2012; Maiden *et al.*, 2013). The ribosomal genes are distributed around the genome, offering some stability against horizonal gene transfer (Jolley *et al.*, 2012; Maiden *et al.*, 2013) and are also under stabilising selection because they encode proteins necessary for bacterial function (Jolley *et al.*, 2012). These traits make the ribosomal genes ideal candidates for a typing scheme as they are robust and unlikely to undergo rapid or substantial changes. The smaller number of genes involved within an rMLST analysis enabled a larger number of isolates to be analysed at a time, with reduced computing capability and produced results more rapidly.

Isolates from the different *S. enterica* subspecies began to cluster together when more than 19 of the rST alleles differed. Therefore, a more conservative number of allelic differences, such as 15 would identify the majority of isolates from the same subspecies, whilst ensuring that conflicts between subspecies classification did not occur. This threshold should, however, be periodically reviewed because as gaps within the diversity of an organism are filled, the number of allelic differences required to identify all members of a species or subspecies can decrease.

Isolates that did not cluster with any known subspecies and could therefore have been representative of novel subspecies can be confirmed as novel subspecies using the new ‘gold standard approach’ (Richter and Rosselló-Móra, 2009) of speciation – ANI (Lee *et al.*, 2016). To identify organisms as the same species an ANI of 95% or greater was necessary (Klappenbach *et al.*, 2007). ANI was comparable (Richter and Rosselló-Móra, 2009) and congruent (Konstantinidis and Tiedje, 2005) to the laboratory-based approach – DDH, which required hybridisation of 70% to identify isolates as the same species (Wayne *et al.*, 1987). DDH had previously been classified as the gold standard of prokaryotic speciation (Wayne *et al.*, 1987) but was too labour-intensive (Gevers *et al.*, 2005), time consuming (Gevers *et al.*, 2005) and error prone (Stackebrandt *et al.*, 2002) for all but a few laboratories to perform (Stackebrandt *et al.*, 2002; Gevers *et al.*, 2005). In contrast, ANI analyses were simple to perform, as online tools have been developed (Lee *et al.*, 2016; Richter *et al.*, 2016). As ANI looked at differences from across the whole genome it was not reliant on a single or small subset of genes remaining consistent across all isolates within a species or subspecies. Therefore, ANI should not be affected by small scales within a genome and should be capable of consistently identifying species and subspecies.

A clear example of the problem with conventional methods was isolate SAL_MA5841AA, which was identified as subspecies II using these methods. Across all levels of genomic typing schemes, all of the genetic methods analysed here – phylogenies, STRUCTURE and ANI confirmed it was a subspecies I isolate. However, reanalysis using Biolog continued to show that it clustered more closely with subspecies II isolates or isolates closely related to subspecies II.

A number of papers have been published which state the need for a genome-based speciation method (Gevers *et al.*, 2005; Chun and Rainey, 2014; Varghese *et al.*, 2015), recommended guidelines have even been published (Gevers *et al.*, 2005; Kim *et al.*, 2014; Chun *et al.*, 2018) in support of this shift away from conventional methods. The use of genome-based methods for the identification of species has become more common within bacterial species. For example, species within other genera, such as *Neisseria* (Bennett *et al.*, 2012) and *Acinetobacter* (Chan *et al.*, 2012) have been identified using genome-based approaches.

In this study it has been demonstrated that speciation and subspeciation of the genus *Salmonella* can and should be performed using WGS-based approaches. Using these approaches five new *S. enterica* subspecies have been confirmed and named with the next available roman numerals, in accordance with current taxonomy (VII, VIII, IX, X and XI) (Grimont and Weill, 2007). Furthermore, *S. enterica* subspecies IIIa was identified as a separate species – *Salmonella arizonae*. The name *S. arizonae* was chosen as arizonae was the historical name for subspecies IIIa before the subspecies were reclassified as roman numerals (Grimont and Weill, 2007). Speciation and subspeciation within the salmonellae should now be performed using the genome-based approaches of rMLST (Jolley *et al.*, 2012) and ANI (Lee *et al.*, 2016), as opposed to the conventional methods of biochemical properties and DDH (Wayne *et al.*, 1987).

5.5 Conclusions

In this study a comprehensive analysis of the genus of *Salmonella* and a genomic methodology to define the species and subspecies was presented. This analysis demonstrated that analyses of biochemical properties for speciation and subspeciation could not accurately define and identify all of the species and subspecies within the genus. It was therefore proposed that genome-based approaches should be utilised instead, as these methods were highly congruent, stable and capable of distinguishing genetic groupings accurately and consistently. For routine speciation and subspeciation rMLST-based typing should be utilised, the majority of isolates would cluster with their species or subspecies with 15 or less allelic differences. For those isolates which do not, ANI could be used in order to confirm species or subspecies. Using WGS-based approaches to speciated and subspeciate *Salmonella* five novel subspecies were confirmed (VII, VIII, IX, X and XI) and *S. enterica* subspecies IIIa was reclassified as *S. arizonae.* The change to utilising WGS-based approaches for speciation and subspeciation within *Salmonella* is in line with global surveillance and reference laboratories which are also switching to WGS-based approaches for the monitoring and routine typing of the salmonellae.

Statement of Authorship for joint/multi-authored papers for PGR thesis

To appear at the end of each thesis chapter submitted as an article/paper

The statement shall describe the candidate's and co-authors' independent research contributions in the thesis publications. For each publication there should exist a complete statement that is to be filled out and signed by the candidate and supervisor **(only required where there isn't already a statement of contribution within the paper itself).**

Title of Paper	An evaluation of speciation and subspeciation of the *Salmonella* genus using whole genome sequencing
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Student Confirmation

Student Name: Madison Pearce		
Performed all analysis, data interpretation, prepared manuscript for publication, constructed and edited all of the figures.		
Signature	Date	

Supervisor Confirmation

By signing the Statement of Authorship, you are certifying that the candidate made a substantial contribution to the publication, and that the description described above is accurate.

Supervisor name and title:		
Supervisor comments:		
Signature	Date	

Chapter Six

A characterisation of *Salmonella enterica* serovar Enteritidis from New South Wales, Australia

Abstract

While *Salmonella* enterica serovar Enteritidis is less prevalent in Australia than it is globally, it is still one of the most common serotypes in Australia and in NSW the notification rates are the second highest in the country. Whole genome sequencing has previously been used to elucidate the population structure of this serovar and is used here to characterise 95 NSW serovar Enteritidis isolates. These isolates were then compared to serovar Enteritidis from Queensland and all of the Australian isolates were compared to isolates from across the globe. The NSW isolates only fell into two of the three clades identified in the Queensland isolates (Clades A and B) and antimicrobial resistance also varied between the states, suggesting that there are regional differences within serovar Enteritidis in Australia. Genomic comparison of Australian and global isolates showed that the genetic content of the Australian serovar Enteritidis isolates are highly admixed with Asian serovar Enteritidis isolates, which supported previous findings that the majority of serovar Enteritidis is imported into Australia from Asia. Within Clade B, however, a lineage consisting of 57 closely related Australian isolates was identified, all of which were still highly susceptible to antimicrobials. The presence of this lineage suggests that there may have been a more recent import of serovar Enteritidis into Australia, which has persisted locally since and is not regularly exposed to antimicrobials. This suggests that more cases of serovar Enteritidis may be locally acquired than had previously been believed.

6.1 Introduction

Every year *Salmonella enterica (S. enterica)* subspecies enterica is responsible for an estimated 94 million cases of gastroenteritis globally (Majowicz *et al.*, 2010), of which an estimated 80.3 million are foodborne (Majowicz *et al.*, 2010). *S. enterica* serovar Enteritidis is the most common cause of human *Salmonella* infection and is responsible for approximately 65% of cases globally (Galanis *et al.*, 2006). The most important vehicle for human infection with serovar Enteritidis appears to be egg consumption, (Louis *et al.*, 1988; Mishu *et al.*, 1994) as there is a strong association between human disease and serovar Enteritidis prevalence in commercial laying hens (Chai *et al.*, 2012; HAVELAAR *et al.*, 2013). In the three days prior to infection a patient with a sporadic serovar Enteritidis infection was over five times more likely to have consumed egg than a healthy control (Braden, 2006). Infection is also associated with consuming food prepared outside of the home (Patrick *et al.*, 2004). This may be caused by the practice of pooling large quantities of eggs for increased food production (Sobel *et al.*, 2000), therefore allowing a small number of infected eggs to contaminate a greater quantity of food, leading to higher exposure levels (Braden, 2006).

Within both the EU (Eurosurveillance editorial team, 2012) and the USA (Center for Emerging and Infectious Diseases, 2016) serovar Enteritidis is the most commonly isolated serovar and is responsible for 48.5% (Eurosurveillance editorial team, 2012) and 16.8% (Center for Emerging and Infectious Diseases, 2016) of human infections respectively. In contrast, serovar Enteritidis accounted for only 5.7% of notifications for human *Salmonella* infection within Australia (Ford *et al.*, 2016) but is still one of the five most common Australian serovars (OzFoodNet Working Group, 2015). Serovar

Enteritidis was, however, responsible for considerably fewer notifications than serovar Typhimurium in Australia, which was responsible for 43.9% (Ford *et al.*, 2016). Serovar Enteritidis may be scarcer in Australia because it is not endemic in commercial Australasian poultry flocks (OzFoodNet Working Group, 2015; Chousalkar *et al.*, 2018).

Data published by the OzFoodNet Working Group demonstrated that the majority of serovar Enteritidis cases in Australia are associated with overseas travel, as only 11% of individuals are believed to have acquired the infection locally, the other 89% had recently travelled overseas (OzFoodNet Working Group, 2015). Of those infections acquired overseas, the majority (86%) were acquired within South East Asia. Most commonly, infected individuals had travelled to Indonesia (62%), followed by Thailand (8%) and Malaysia (5%) (OzFoodNet Working Group, 2015).

A recent examination of clinical human isolates of serovar Enteritidis from Queensland (Australia) identified three genomic clades, defined as Clade A, B and C (Graham *et al.*, 2018). Clades A and C were composed of endemic Australian strains, as individuals infected with these strains had no travel history and environmental strains from Queensland were also members of these highly divergent clades. This suggested that isolates from these clades were locally acquired (Graham *et al.*, 2018). In contrast Clade B was a global clade that primarily consisted of strains associated with individuals that had recently travels to Asia (Graham *et al.*, 2018). This clade corresponded to the previously observed Lineage 5 (Deng *et al.*, 2014), which was

predominantly composed of Asian isolates, further supporting the conclusions drawn within the Queensland study (Graham *et al.*, 2018).

WGS is now recognised as the gold standard to investigate genome evolution and population genetics of *Salmonella*, including serovar Enteritidis (Deng *et al.*, 2014; Langridge *et al.*, 2015; Feasey *et al.*, 2016; Graham *et al.*, 2018). Previous gold standard methods for the analysis of serovar Enteritidis isolates that relied upon a subset of genes or genetic signals, including PFGE, have struggled to elucidate the full diversity of this relatively homogenous serovar (Olson *et al.*, 2007; Allard *et al.*, 2013). For example, analysis of 106 isolates that had the same PFGE profile, revealed thousands of SNPs and multiple variable genes (366 genes) (Allard *et al.*, 2013), demonstrating the depths of diversity that can be lost when isolates are analysed using a subset of genes. WGS has been used in the analysis of the serovar Enteritidis lineage, to determine how it was related to its close relatives (serovars Gallinarum/Pullorum and Dublin). Furthermore, WGS has been used to identify prevalent lineages of serovar Enteritidis and the population structure of these lineages (Deng *et al.*, 2014; Feasey *et al.*, 2016). These analyses have revealed lineages with specific geographical or epidemiological characteristics, such as wildlife and environmental sources (Deng *et al.*, 2014; Feasey *et al.*, 2016), demonstrating the utility of WGS for the characterisation of serovar Enteritidis isolates.

It is mandatory to report all *Salmonella* isolates within Australia (Miller *et al.*, 2004; OzFoodNet Working Group, 2017). Serovar Enteritidis is of particular importance because it is currently absent from Australian poultry flocks (OzFoodNet Working

Group, 2015; Chousalkar *et al.*, 2018) and the majority of cases are believed to be travel associated (OzFoodNet Working Group, 2015). It is therefore necessary to understand the origins of these isolates, to facilitate surveillance and for epidemiological purposes, for which WGS has been demonstrated to be beneficial (Dallman *et al.*, 2016). Within the Australian states/territories NSW has the second highest number of total and locally-acquired notifications for serovar Enteritidis and the third highest for Overseas-acquisition (OzFoodNet Working Group, 2015).

In this study the properties of 95 serovar Enteritidis isolates from NSW were examined, using WGS. Acquired AMR genes, chromosomal point mutations that increase antibiotic resistance, plasmids and SPIs were all examined. Furthermore, the NSW isolates were compared with a dataset of isolates from Queensland, which had undergone similar examinations (Graham *et al.*, 2018), in order to determine the diversity of serovar Enteritidis across Australia. For example, the comparison can be used to determine if the previously observed Australian clades were state restricted or if the diversity was relatively uniform across the country. These isolates were also compared to global isolates from Africa, Asia, Europe, North America and South America to place them in a global context. Comparisons with global isolates were conducted to widen the knowledge of serovar Enteritidis and to provide insight into the source of the NSW isolates and to determine from where isolates may be imported. These isolates enabled a more detailed examination of the link between travel to Asia and serovar Enteritidis cases within Australia.

6.2 Materials and Methods

6.2.1 Collection and curation NSW, Australia isolates

Initially, 97 clinical isolates that had been identified as *S. enterica* serovar Enteritidis by conventional serotyping in NSW, Australia were collected and WGS. The raw sequence files were then uploaded to the Enterobase (http://enterobase.warwick.ac.uk) assembly pipeline, where they underwent SPAdes (Bankevich *et al.*, 2012) assembly using the parameters established by the Enterobase team. The SISTR tool (Yoshida *et al.*, 2016) was then used in order to confirm the serovar typed by conventional serotyping. Of the 97 isolates 95 were identified as serovar Enteritidis using SISTR, the other two isolates (NSW094 and NSW115) were respectively identified as serovar Give and one of serovar Pensacola/ Sangalkam/ subspecies II serovar (antigenic formulae: 1,9,12:g,m,[s],t:[1,5,7]:[z42]). The two isolates that were not identified as serovar Enteritidis were excluded from the rest of the analysis, which left a dataset of 95 serovar Enteritidis isolates from New South Wales. Assemblies of all of these isolates are available from both Enterobase (http://enterobase.warwick.ac.uk) and from Pubmlst (Jolley and Maiden, 2010) (https://pubmlst.org/salmonella/) (Appendix Q).

6.2.2 Examination of serial isolates

Eight of the 95 NSW isolates were serial colony picks (4 patients, 2 colony picks from each) and two isolates were from the same household (Appendix R). Isolates were examined to determine how closely related these colony picks were. The results were used to annotate a NJTree of all 95 NSW isolates. A distance matrix was calculated using the genome comparator tool found on the $BIGS_{DB}$ (Jolley and Maiden, 2010) platform of pubmlst, the distance matrix was calculated using the cgMLST (Alikhan *et*

al., 2018) scheme developed by Enterobase. The matrix was converted into a NJTree (Saitou and Nei, 1987) using SplitsTree (Huson and Bryant, 2006) and the NJTree was annotated using the ITOL online tool (Letunic and Bork, 2016).

6.2.3 Identification of antimicrobial resistance genes (AMR)

To detect AMR genes the WGS data was run through the ResFinder-3.1 pipeline (Zankari *et al.*, 2012), which identified acquired AMR genes and chromosomal mutations within bacterial genomes. The acquired genes may confer resistance to antimicrobial agents including: aminoglycosides, beta-lactams, colistins, quinolones, fosfomycins, fusidic acid, glycopeptides, MLS (macrolide, Lincosamide and Streptogramin B), nitroimidazoles, oxazolidinones, phenicols, rifampicins, sulphonamides, tretracyclines and trimethrophrims (Zankari *et al.*, 2012). The known chromosomal point mutations occured in *23S* (macrolides), *pmrB* and *pmrA* (colistin)*, 16S_rrsD* (spectinomycin), *gyrA,* and *gyrB* (fluoroquinolones) and *parC* and *parE* (quinolones) (Zankari *et al.*, 2012)*.* ResFinder-3.1 was used to search for acquired resistance genes and chromosomal point mutations in the 95 NSW isolates (Zankari *et al.*, 2012). For the chromosomal mutations searches were run on the *Salmonella* database for known mutations with the default parameters, which were: (i) a threshold of 90% or greater percentage identity and (ii) a 60% minimum length. For the acquired antimicrobial resistance genes, all ResFinder-3.1 databases were selected and the default parameters were the same as for the chromosomal mutations searches. The results were used to annotate a cgMLST NJTree of all 95 NSW isolates using ITOL (Letunic and Bork, 2016).

6.2.4 Identification of plasmids

To detect plasmids within the NSW isolates the PlasmidFinder2.0 (Carattoli *et al.*, 2014) database was used. Both the Enterobacteriaceae and Gram-positive databases were searched for plasmid matches. The default parameters were used for these searches, these were: (i) a threshold of 95% or greater percentage identity and (ii) a 60% minimum coverage. Plasmids identified within the NSW isolates were analysed individually using ResFinder-3.1 (Carattoli *et al.*, 2014) for acquired AMR genes, to confirm if the genes were on the plasmid, this analysis was run on default parameters. The results were used to annotate a cgMLST NJTree of all 95 NSW isolates using ITOL (Letunic and Bork, 2016).

6.2.5 Identification of *Salmonella* pathogenicity Islands (SPIs)

SPIs were clusters of genes that enabled the bacteria to invade, survive and spread throughout a host, which were believed to be acquired through horizontal gene transfer. There were 22 identified SPIs throughout the *Salmonella* genus, 1 of which was specific to *Salmonella bongori*. The genes from the SPIs were extracted from complete genomes in NCBI. SPIs 1, 2, 3, 4, 5, 6, 9, 10, 13, 14, 16 and 17 were from P125109 (Enteritidis) (Thomson *et al.*, 2008); SPIs 7, 8, 15 and 18 were from CT18 (Typhi) (Parkhill *et al.*, 2001); SPI 11 was from SC-B67 (Choleraesuis) (Chiu *et al.*, 2005); SPI 12 was from SL1344 (Typhimurium) (Kroger *et al.*, 2012); SPI 19 was from 287/91 (Gallinarum) (Thomson *et al.*, 2008); SPIs 20 and 21 were from 62:z4,z23:-(-)(*S. arizonae*) and SPI 22 was from NCTC12419 (*S. bongori*) (Fookes *et al.*, 2011).

BLAST searches were conducted on the NSW genomes for the SPIs. For a match (i) the statistical significance of an alignment had to be greater than 1.0E-3; (ii) the number of BLAST hits (alignments) had to be over 20; (iii) the length of the initial word of the alignment had to be over 11 and (iv) the length of the first High-scoring Segment Pair of a BLAST hit had to be over 33. For the BLAST matches to be classed as a SPI they had to occur within the same genomic region and no more than three genes could be missing and more than 85% of the genes within the SPI had to be present.

6.2.6 Comparison of NSW isolates with Queensland Isolates

A dataset of 217 serovar Enteritidis isolates from Queensland (Graham *et al.*, 2018) were the focus of a recent paper, of these 217 isolates 195 were available from Enterobase (http://enterobase.warwick.ac.uk). When analysed with SISTR (Yoshida *et al.*, 2016) four of these isolates were not identified as serovar Enteritidis and were therefore excluded. This left a dataset of 191 Queensland isolates for comparison with the 95 NSW isolates (Appendix Q).

A distance matrix of the cgMLST (Alikhan *et al.*, 2018) profiles of these isolates was created using the BIGS$_{DB}$ genome comparator tool (Jolley and Maiden, 2010) and was converted into a NJTree (Saitou and Nei, 1987) using SplitsTree (Huson and Bryant, 2006). The presence of resistance genes, plasmids and SPIs was then compared across the two datasets. The NJTrees were annotated using the ITOL website (Letunic and Bork, 2016). A microreact (Argimón *et al.*, 2016) project was also created to enable visualisation of these isolates on a map and for interactive exploration of the data.

6.2.7 Comparison of NSW isolates with global isolates

A dataset of global isolates was created for the comparison of the NSW isolates with all isolates that were identified as serovar Enteritidis by their metadata and that had a country specified within their metadata were downloaded (25,968) from Enterobase (6/11/2018). These isolates were then analysed using SISTR (Yoshida *et al.*, 2016) to confirm the typing of the serovar Enteritidis isolates, any which were not also identified as serovar Enteritidis by the SISTR (Yoshida *et al.*, 2016) analysis were removed. From the remaining isolates up to 100 per continent were selected for Africa, Asia, Europe, North America and South America. Isolates were selected for global diversity by selecting an equal number of isolates, or as many as were available, from every country which had isolates available were selected. Isolates from Oceania were also split into regions, therefore 100 isolates from an analysis into Enteritidis in Queensland were selected and all other Oceania isolates were also included. The isolates that were representative of each country or region were selected randomly. This created a dataset of: 59 African isolates, 100 Asian, 100 European, 100 North American, 100 South American, 6 Oceanian (random isolates in Enterobase), 100 from Queensland and 95 from NSW (Appendix Q).

A cgMLST based distance matrix was created for these 660 isolates using the BIGS$_{DB}$ genome comparator tool (Jolley and Maiden, 2010) and was converted into a NJTree (Saitou and Nei, 1987) using SplitsTree (Huson and Bryant, 2006). This tree was annotated using the ITOL website (Letunic and Bork, 2016). In order to confirm the clusters observed within the global comparisons minimum spanning trees (Edmonds, 1967) were constructed using GrapeTree (Zhou *et al.*, 2018), which is capable of

reconstructing genetic relationships even when there is missing data (Zhou *et al.*, 2018). A microreact (Argimón *et al.*, 2016) project was also created to enable further visualisations of these isolates.

The Oceanian isolates (95 NSW, 191 Queensland and 6 other) were also compared to isolates from Asia, Europe, North American and South America separately. For this analysis isolates were divided into their respective continents and up to 20 serovar Enteritidis isolates, or as many as were available, from each country that had serovar Enteritidis isolates in Enterobase were randomly selected or 200 isolates from across the continent were randomly selected, depending on which dataset was bigger. Therefore, the Oceanian isolates were compared with 245 Asian, 229 European, 200 North American and 200 South American isolates. The sizes of the datasets were increased to help confirm the findings observed within the analysis of the 660 isolates. Distance matrices based on cgMLST were also created for these comparisons using the BIGS$_{DB}$ genome comparator tool (Jolley and Maiden, 2010), were converted into NJTrees (Saitou and Nei, 1987) using SplitsTree (Huson and Bryant, 2006) and were annotated using ITOL (Letunic and Bork, 2016). Minimum spanning trees (Edmonds, 1967) were also created using GrapeTree (Zhou *et al.*, 2018) for these analyses to confirm clusters observed within the NJTrees (Saitou and Nei, 1987). Microreact (Argimón *et al.*, 2016) projects were created for all of the comparisons between the Oceanian isolates and the other continents.

6.3 Results

6.3.1 Serial colony picks in the NSW isolates

Construction of a NJTree (Saitou and Nei, 1987) revealed that the NSW isolates belonged to Clades A (5) and B (90) (Graham *et al.*, 2018); however, no isolates that belonged to Clade C (Graham *et al.*, 2018) were identified in this dataset (Figure 6.1). The Clade A isolates were: 17679, 17688, 17721, 17706 and 17710. Of the 95 NSW isolates eight were serial isolates picked from four patients (two from each patient) and two were household associated cases (Figure 6.1a). The serial or household isolates always belonged to the same clade and were all closely related to their counterpart. The household isolates and six serial isolates (three patients) were most closely related, the other two serial isolates (one patient) were separated by a single isolate and were therefore still very closely related. The serial isolates 17679 and 17721 in Clade A (Figure 6.1a), which were not most closely related were isolated a considerable period of time apart (Appendix R). Isolates 17663 and 17660 shared their branch with a third highly closely related (isolate 17647) (Figure 6.1a), despite being isolated on the same day (Appendix R).

6.3.2 AMR genes in the NSW isolates

The 95 NSW isolates (including the four serial colony picks) were examined for acquired AMR genes (Figure 6.1b). All of the isolates had copies of the aminoglycoside genetic resistance determinant gene, *aac(6')-Iaa (*Appendix S). Other aminoglycoside resistance genes were also detected: *aph(6)-Id, aph(3'')-Ib, aadA1* and *aadA22*. The AMR genes *aph(6)-Id* and *aph(3'')-Ib*, always occurred together and were identified within 7 isolates, while *aadA1* and *aadA22* were both found only once,

in separate isolates. The beta-lectam resistance genes *bla*$_{TEM-1B}$ and *bla*$_{CTX-M-55}$ were found fourteen times and once respectively. Fosfomycin and trimethoprim resistance were both quite rare, only been found in one isolate each (17678 and 17683 respectively). Sulphonamide genetic resistance determinants were found in seven isolates, all of which had acquired the *sul2* gene. The Tetracycline genetic resistance determinant was one of the more commonly acquired genes, as *tet(A)* was identified in thirteen isolates. The most resistant isolates (17631, 17666 and 17698) had six acquired AMR determinant genes (*aac(6')-Iaa, aph(6)-Id, aph(3")-Ib, bla*$_{TEM-1B}$*, sul2* and *tet(A)*), which can provide resistance to aminoglycosides, beta-lactams, sulphonamides and tetracyclines.

Isolates were also examined for chromosomal point mutations associated with the genetic resistance determinants (Figure 6.1c). 52 isolates had mutations within the *gyrA* gene that are associated with increased quinolone resistance. Four different point mutations were detected, *gyrA* p.D87N, *gyrA* p.D87G, *gyrA* p.D87Y and *gyrA* p.S83Y, in 29, 4, 16 and 3 isolates respectively. Isolates 17631, 17666 and 17698 all also carried a *gyrA* point mutation and therefore had genetic determinants suggesting quinolone resistance. There were 35 isolates (36.8%) which only had the AMR gene *aac(6')-Iaa*. A further 41 (43.2%) isolates had the AMR gene *aac(6')-Iaa* and one other AMR associated gene, of those 35 had *gyrA* point mutations and 6 had copies of *tet(A)*. The five Clade A isolates only carried the aminoglycoside resistance determinant gene *aac(6')-Iaa.*

6.3.3 Plasmids in the NSW isolates

The majority of the NSW isolates carried at least one plasmid (78 isolates 82%) (Figure 6.1d). Plasmids of groups IncFIB(S), IncFII(S), IncFII(pHN7A8), IncI1, IncX1 and Col156 were all identified within the NSW isolates. The most common plasmid types were IncFIB(S) and IncFII(S), which were present in 74 (78%) and 76 (80%) isolates respectively. Incl1 and IncX1 plasmids were present in 5 (5%) and 28 (29%) isolates respectively, while IncFII(pHN7A8) and Col156 were only present in one isolate each. Five plasmids were identified in isolate 17623, these were: IncFIB(S), IncFII(S), IncFII(pHN7A8), IncI1 and IncX1. None of the five Clade A isolates carried any plasmids. No resistance genes were found in any of the plasmids when they were searched for resistance genes using ResFinder3.1 (Zankari *et al.*, 2012).

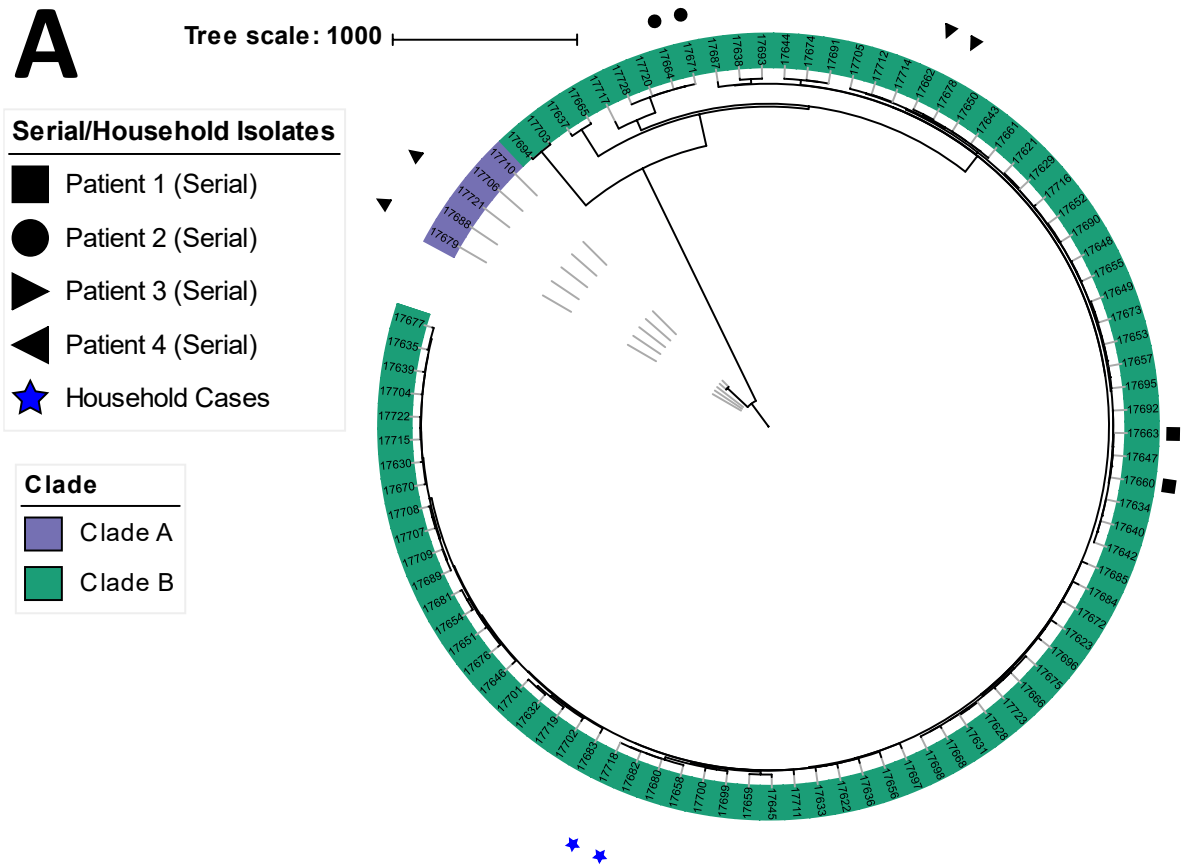


Figure 6.1: NJTree of NSW isolates annotated with the serovar Enteritidis showing serial and household isolates (A), acquired resistance genes (B), chromosomal point mutations (C) and plasmids (D) A NJTree of 95 serovar Enteritidis isolates from New South Wales. The tree was constructed using cgMLST alleles and was annotated using ITOL.

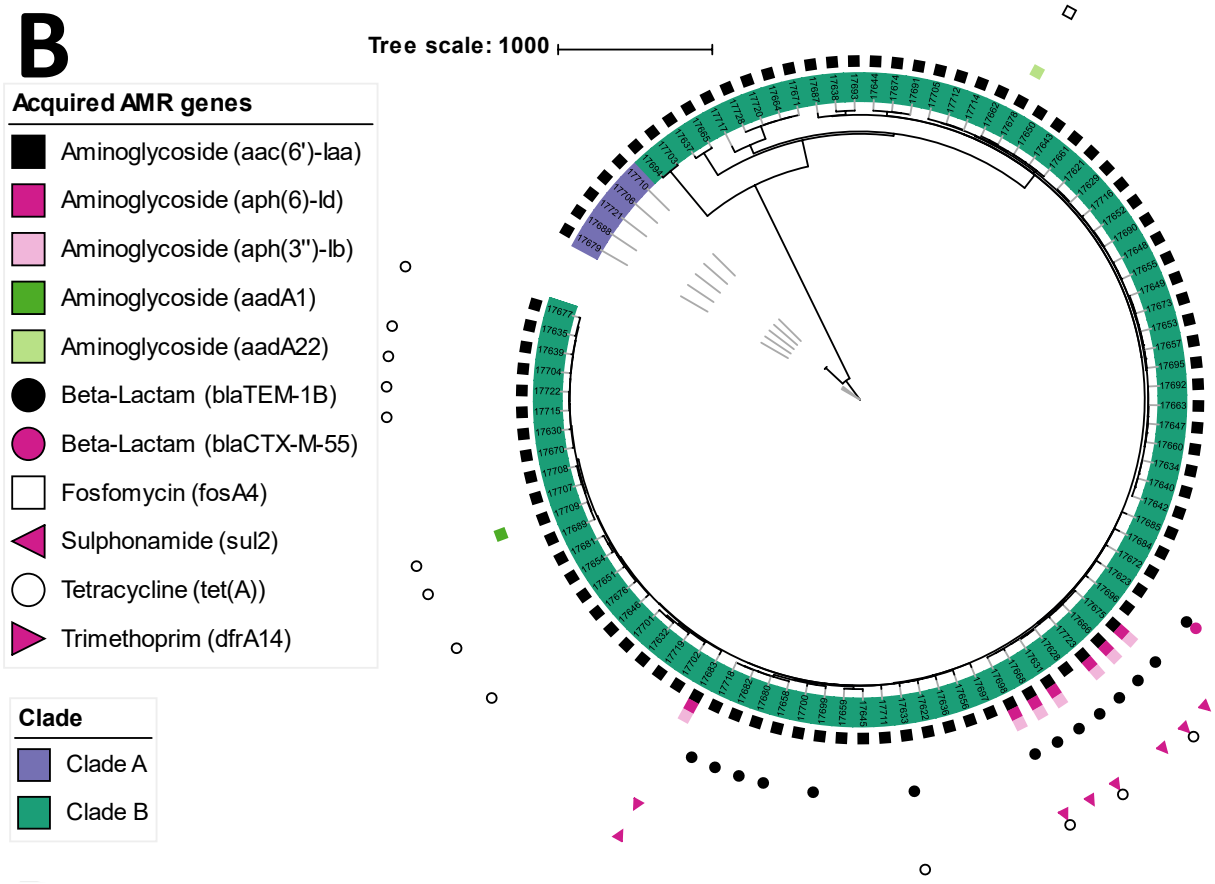


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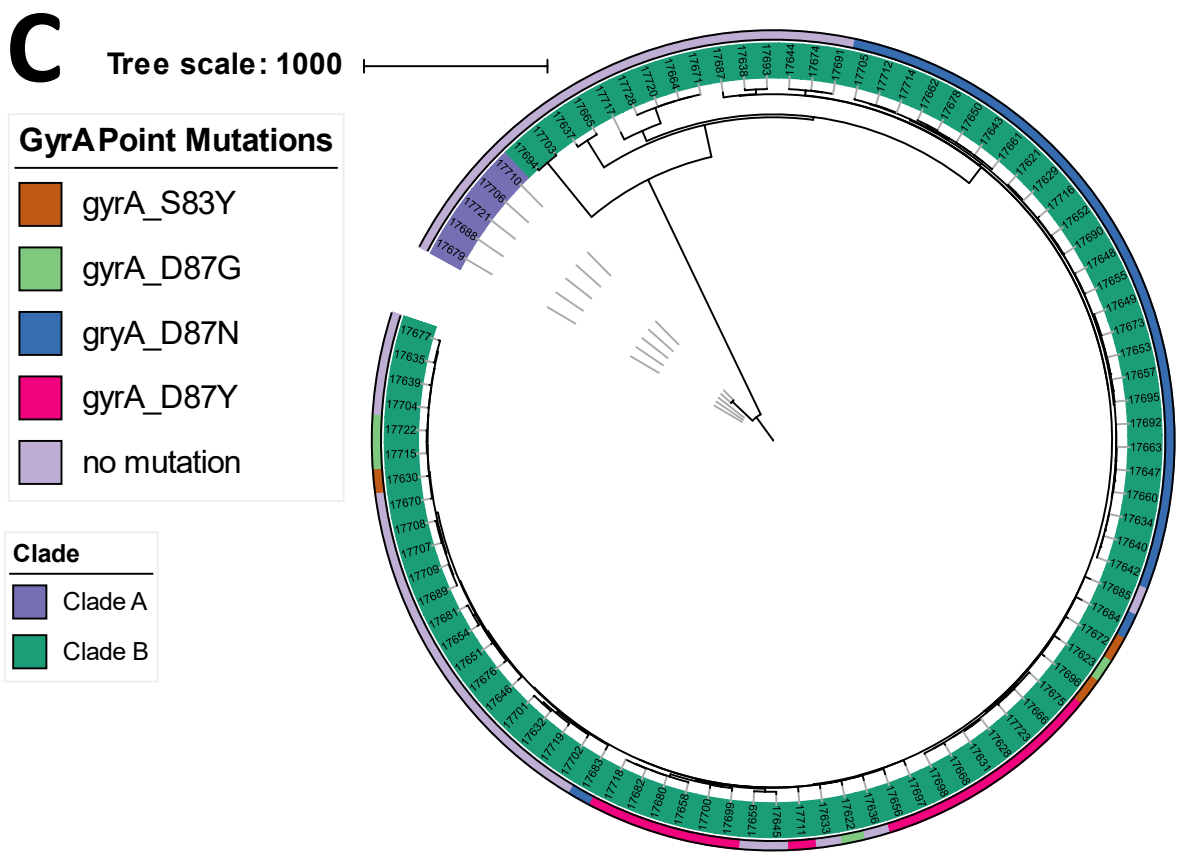


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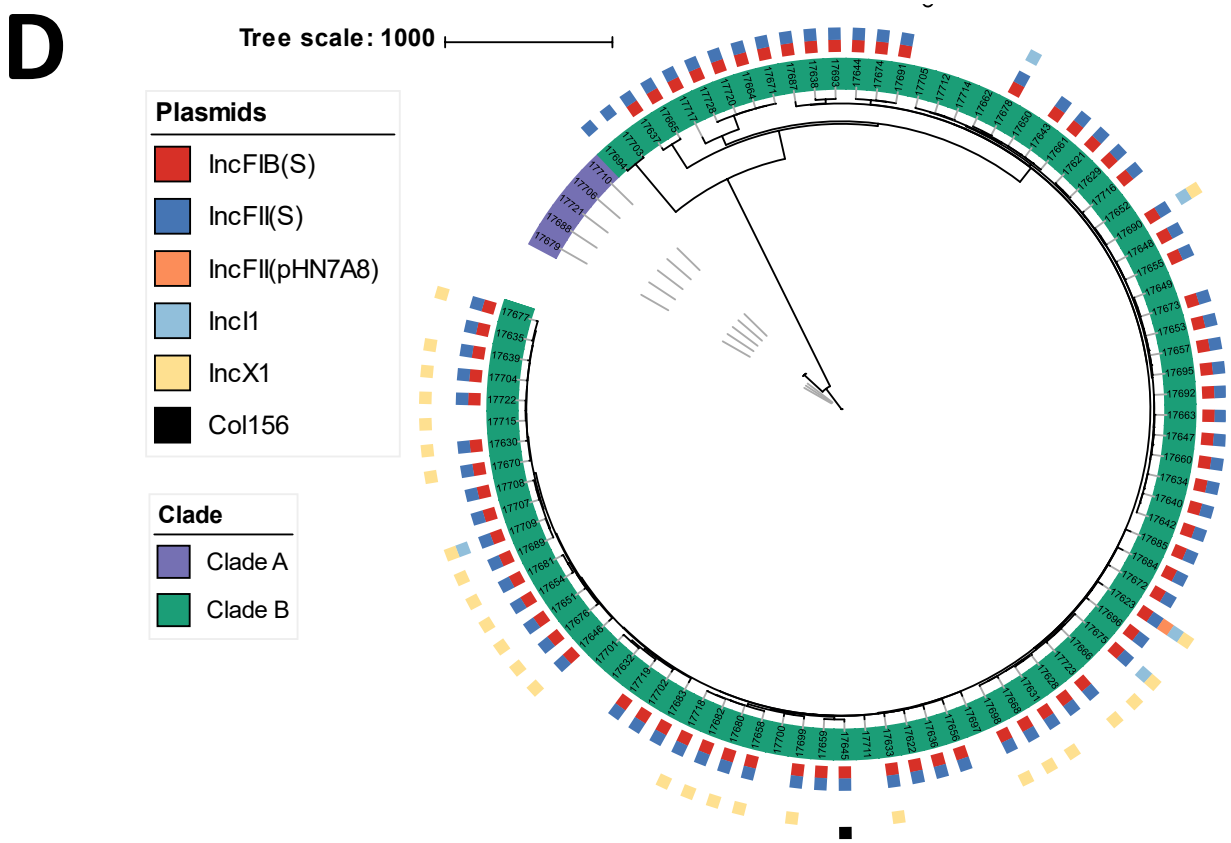


Figure 6.1: NJTree of NSW isolates annotated with the serovar Enteritidis showing serial and household isolates (A), acquired resistance genes (B), chromosomal point mutations (C) and plasmids (D) A NJTree of 95 serovar Enteritidis isolates from New South Wales. The tree was constructed using cgMLST alleles and was annotated using ITOL.

A: Two serial isolates were taken from four patients (annotated with a black square, circle, right facing and left facing triangle) and two isolates were household isolates (annotated with a blue star). All of the isolates from the serial and household isolates belonged to the same clade and were highly related. Six of the serial isolates (three patients) were most closely related to each other, while the other two (one patient) were separated by a single isolate. The household isolates were also most closely related.

B: Acquired resistance genes identified using ResFinder3.1. Aminoglycoside resistance genes were annotated with coloured squares (black, dark pink, light pink, dark green and light green); beta-lactam resistance genes were annotated with coloured circles (black and dark pink); fosfomycin resistance was annotated with a white square; sulphonamide resistance was annotated with a dark pink left-pointing triangle; tetracycline resistance was annotated with a white circle and trimethoprim resistance was annotated with a dark pink right-pointing triangle. All isolates belonging to Clade A and that were ancestral to the rest of Clade B only carried the aminoglycoside resistant gene *aac 6')-laa* (black square). In the rest of the isolates resistance varied from one AMR gene (*aac(6')-laa*) up to 6 different AMR genes.

C: Chromosomal point mutations identified using ResFinder3.1. Isolates with no point mutations are labelled with light purple. All of the chromosomal point mutations occurred within the *gyrA* gene. Four different changes in the *gyrA* gene were observed: p.S83Y (brown), p.D87G (light green), p.D87N (blue) and p.D87Y (pink). No point mutations were observed in the Clade A isolates or the ancestral Clade B isolates. None of the isolates carried more than one point mutation within the *gyrA* gene.

D: Plasmids were identified using PlasmidFinder2.0. The plasmids that were found included IncFIB(S) (red), IncFII(S) (dark blue), IncFII(pHN7A8) (orange), Incl1 (light blue), IncX1 (yellow) and Col156 (black). No plasmids were observed in the Clade A isolates, the majority of the Clade B isolates carried two or more plasmids. The most common plasmid was IncFII(S), closely followed by IncFIB(S), while both IncFII(pHN7A8) and Col156 both only occurred. One isolate carried five plasmids.

6.3.4 SPIs in the NSW isolates

SPIs 1, 2, 3, 4, 5, 6, 9, 10, 13, 14 and 16 were present and complete in all of the isolates, with the exception of SPI-5 which had one gene missing in isolate 17694 and 17703. While SPIs 7, 8, 12, 15, 18, 20 and 22 were absent in all of the isolates.

SPI-11 was present in two very closely related Clade B isolates 17637 and 17665 and was missing in all of the other NSW isolates. SPI-17 was present in all of the Clade B isolates but was missing in the Clade A isolates. SPI-19 was not intact in any of the NSW isolates, however all of the genes were present in the Clade A isolates 17679, 17688,17706, 17710 and 17721 and two of the Clade B isolates 17694 and 17703. Two of the Clade A isolates (17706 and 17710) also had nearly intact copies of SPI-21. Both of these isolates were missing 2 of the 18 genes found in SPI-21, suggesting that the plasmid had possibly become truncated.

6.3.5 Comparison of NSW isolates with Queensland Isolates

The 95 NSW isolates were compared with 191 isolates that were part of a recent study on serovar Enteritidis in Queensland (Graham *et al.*, 2018) (Figure 6.2). The Queensland isolates were split into three Clades – A, B and C. Of the 195 Queensland isolates available in Enterobase 66 belonged to Clade A, 108 to Clade B and 17 to Clade C. Within the 95 NSW isolates 5 belonged to Clade A, 90 to Clade B and no Clade C isolates were identified (Figure 6.2a). The NSW isolates 17694 and 17703 were ancestral to the other Clade B isolates.

None of the Clade A or Clade C isolates carried any point mutations in the *gyrA* gene (Figure 6.2b). Furthermore, NSW isolates 17694, 17703, 18075, 17637, 17665, 17717, 18058, 18111, 17728, 17720, 17664 and 17671 were all Clade B isolates but were ancestral to the other Clade B isolates and these isolates also had no point mutations in the *gyrA* gene.

These isolates also had no acquired AMR genes, with the exception of *aac(6')-Iaa*, which was present in all isolates (Figure 6.2c). One Clade A isolate (18130), which was from the Queensland dataset, had acquired a $bla_{TEM\text{-}1B}$ beta-lactam resistance gene. Resistance in the Clade B isolates was highly variable, with some isolates carrying only one or two chromosomal point mutations and/or acquired resistance determinant genes, while others carried up to five acquired resistant determinant genes. Resistance within the Clade B isolates did appear to cluster, with resistance to the same genes occurring in the same sections of the NJTree (Figure 6.2c) (Saitou and Nei, 1987).

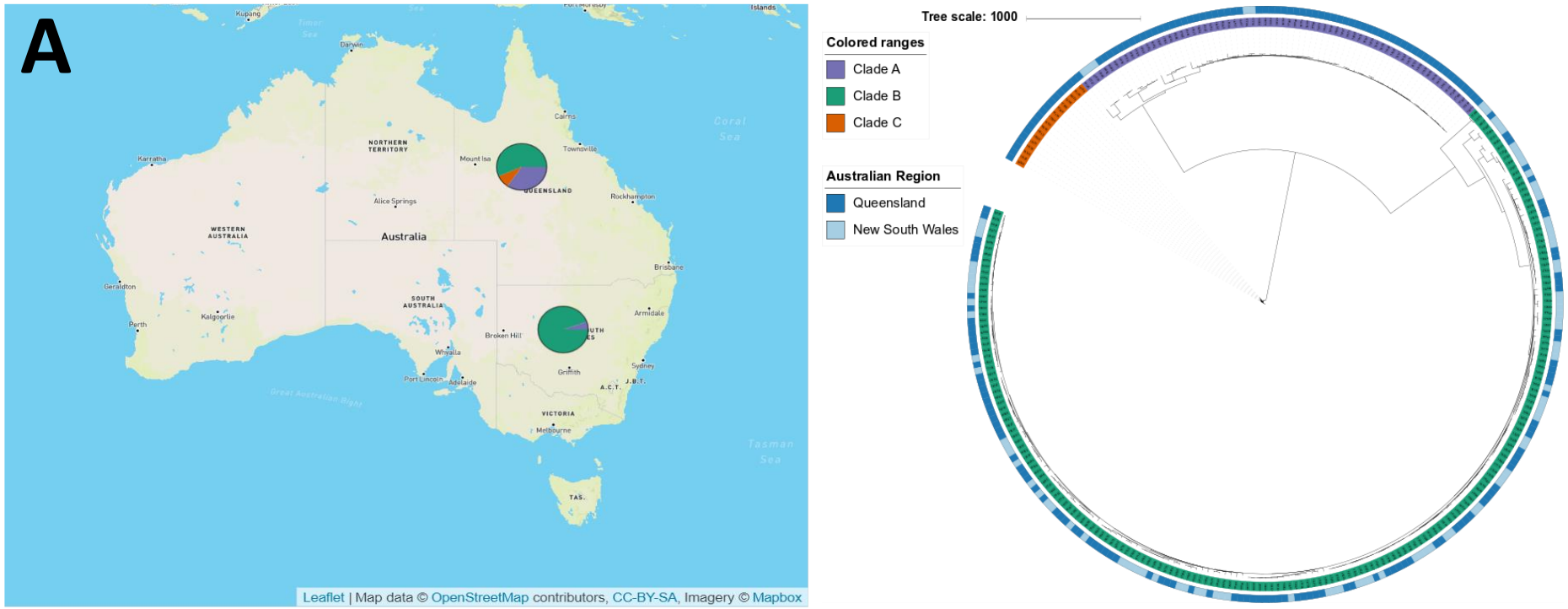


Figure 6.2: NJTree of NSW and Queensland isolates, comparing the spread of isolates (A), annotated with acquired resistance genes (B) and annotated with chromosomal point mutations (C). A NJTree of 95 serovar Enteritidis isolates from New South Wales and 191 isolates from Queensland. The tree was constructed using cgMLST alleles and was annotated using ITOL.

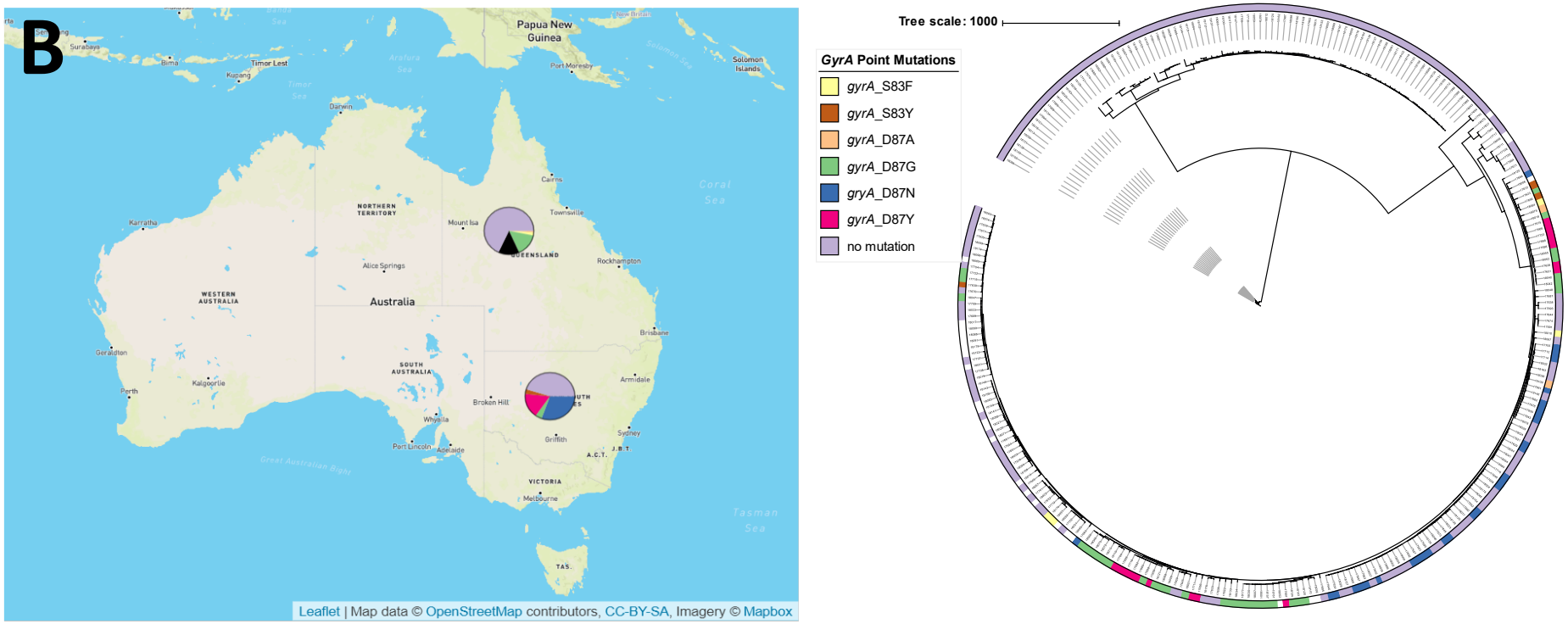


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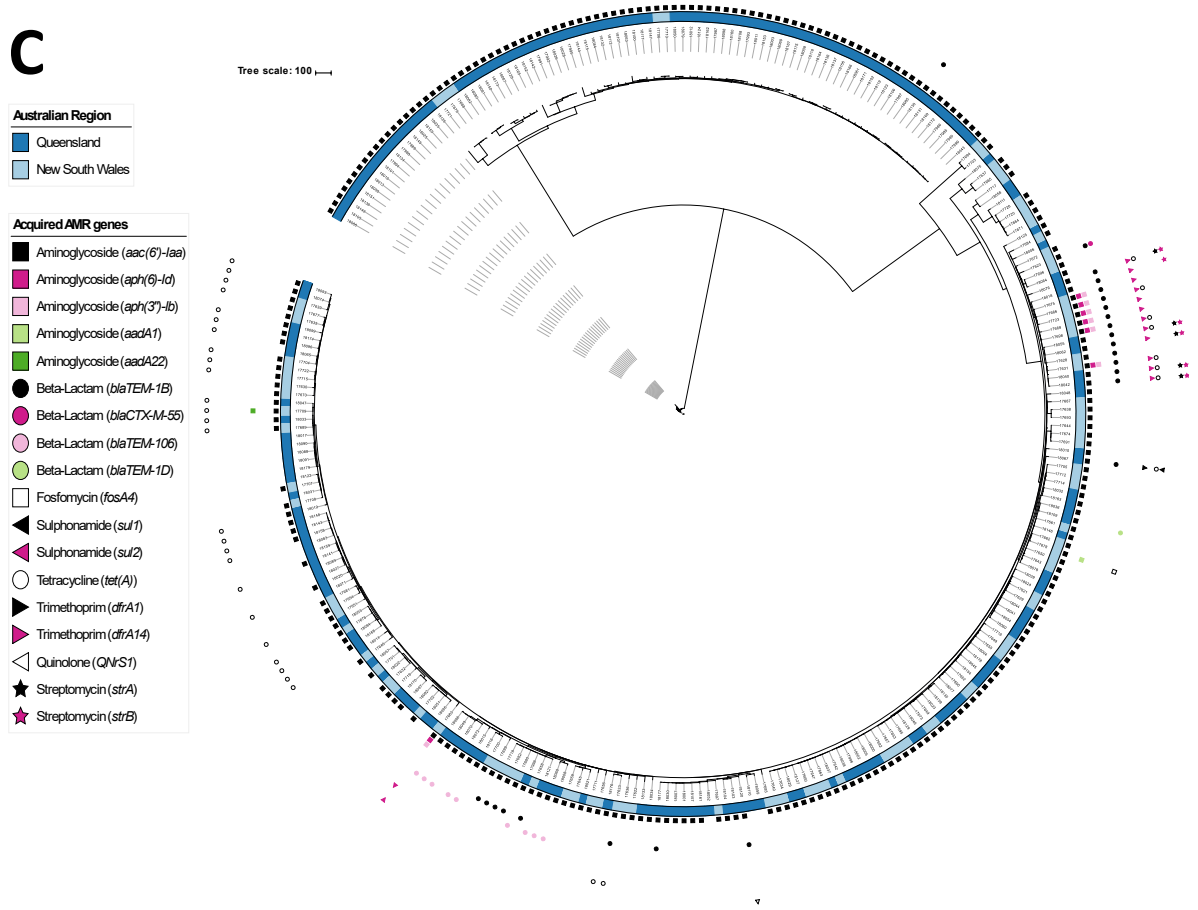


Figure 6.2: NJTree of NSW and Queensland isolates, comparing the spread of isolates (A), annotated with acquired resistance genes (B) and annotated with chromosomal point mutations (C). A NJTree of 95 serovar Enteritidis isolates from New South Wales and 191 isolates from Queensland. The tree was constructed using cgMLST alleles and was annotated using ITOL.

A: The clades identified within the study of Queensland isolates were used to annotate the NSW isolates. Within the NSW isolates none belonged to Clade C suggesting that Clade C is not observed within NSW. Five NSW isolates belonged to Clade A and were admixed with the Queensland isolates. The rest of the NSW isolates (90) belonged to Clade B. The Clade B isolates were highly admixed between NSW and Queensland, suggesting that there was no region-based restriction of movement within the Clade B isolates.

B: Chromosomal point mutations in the NSW isolates were identified through ResFinder3.1 and resistance gene information for the Queensland isolates was obtained from the study. Isolates where no mutation was found are marked in light purple and where information was missing are marked in white. All of the mutations occurred within the *gyrA* gene but six different point mutations were observed: pS83F (yellow), p.S83Y (brown), p.D87A (orange), p.D87G (green), p.D87N (blue) and p.D87Y (pink). None of the Clade A and C isolates carried any point mutation in the *gyrA* gene and neither did the ancestral Clade B isolates. No more than one point mutation was observed within the *gyrA* gene. The most common point mutation was D87G and the least common was D87A.

C: Acquired resistance genes in the NSW isolates were identified through ResFinder3.1 and resistance gene information for the Queensland isolates was obtained from the study. Acquired AMR gene information was not available for those isolates that have no marked resistance information. Aminoglycoside resistance genes were annotated with coloured squares (black, dark pink, light pink, dark green and light green); beta-lactam resistance genes were annotated with coloured circles (black, dark pink, light pink and dark green); fosfomycin resistance was annotated with a white square; sulphonamide resistance genes were annotated with left-pointing triangles (black and dark pink); tetracycline resistance was annotated with a white circle; trimethoprim resistance genes were annotated with right-pointing triangles (black and dark pink); quinolone resistance was annotated with a white left-pointing triangle and streptomcycin resistance genes were annotated with coloured stars (black and dark pink). None of the Clade A and C isolates carried any resistance genes except

for *aac(6')-Iaa*, with the exception of one Clade A isolate which carried a beta-lactam resistance gene. The Clade B isolates were highly variable, with some carrying only one resistance gene, while others carried up to six. There was no observable variation between the NSW and Queensland isolates in acquired AMR genes.

None of the Clade A isolates carried any plasmids within the NSW dataset, this was similar to the Queensland dataset, which found that the majority of plasmids were within Clade B isolates. Both datasets identified IncFIB(S) (74 NSW isolates) as one of the most common plasmids within the isolates, although plasmid IncFII(S) (76 NSW isolates), which was also observed at high levels in the NSW isolates, was not found within the Queensland dataset. IncX1 was also found in both datasets; however, resistance was not found in the plasmids of the NSW isolates, whereas plasmids were commonly associated with resistance in the Queensland isolates.

SPIs were highly congruent between the two datasets. As with the Queensland dataset SPI-17 was present in Clade B isolates but was absent in Clade A isolates. While, SPI-19 was present in the Clade A isolates and absent in the Clade B isolates in both datasets, with the exception of the NSW isolates 17694 and 17703. SPIs 1, 2, 3, 4, 5, 6, 9, 10, 13, 14 and 16 were present in both datasets, while SPIs 7, 8, 12, 15, 18, 20 and 22 were absent in all. SPI-21 was also variable between the datasets, as it was missing in all of the Queensland isolates but was present in two Clade A isolates from NSW, although two genes were missing in these isolates.

This data is also available for interactive exploration via the microreact (Argimón *et al.*, 2016) project: https://microreact.org/project/HJkdmnakE

6.3.6 Comparison of NSW isolates with global isolates

A cgMLST NJTree was constructed to compare the 95 NSW isolates with representatives of serovar Enteritdis from across the globe, up to 100 isolates were taken from each continent, with the exception of Oceania, where 6 Oceanian isolates and 100 Queensland isolates were used (Figure 6.3). Clade C consisted entirely of Queensland isolates and Clade A was predominantly composed of Oceanian isolates (5 NSW), however there were two non-Oceanian isolates, one from Europe and one from Asia (17549 and 17407 respectively) that were present in Clade A. Clade B was composed of isolates from across the continents (90 NSW). African isolates were predominantly ancestral to the other Clade B isolates, although some were admixed with the European clade. North American isolates formed two distinct clades that had little admixture with isolates from other continents. The South American isolates also formed a distinct clade that had very little admixture. Asian isolates formed two clades, one of which was small and ancestral to the majority of Clade B isolates, the other Asian clade was highly admixed with the Oceanian isolates. The results were highly congruent between the NJTrees (Figure 6.3) and the minimum spanning trees produced using GrapeTree (Zhou *et al.*, 2018) (Appendix T).

This data is also available for interactive exploration via the microreact (Argimón *et al.*, 2016) project: https://microreact.org/project/Hk2iiCzb4

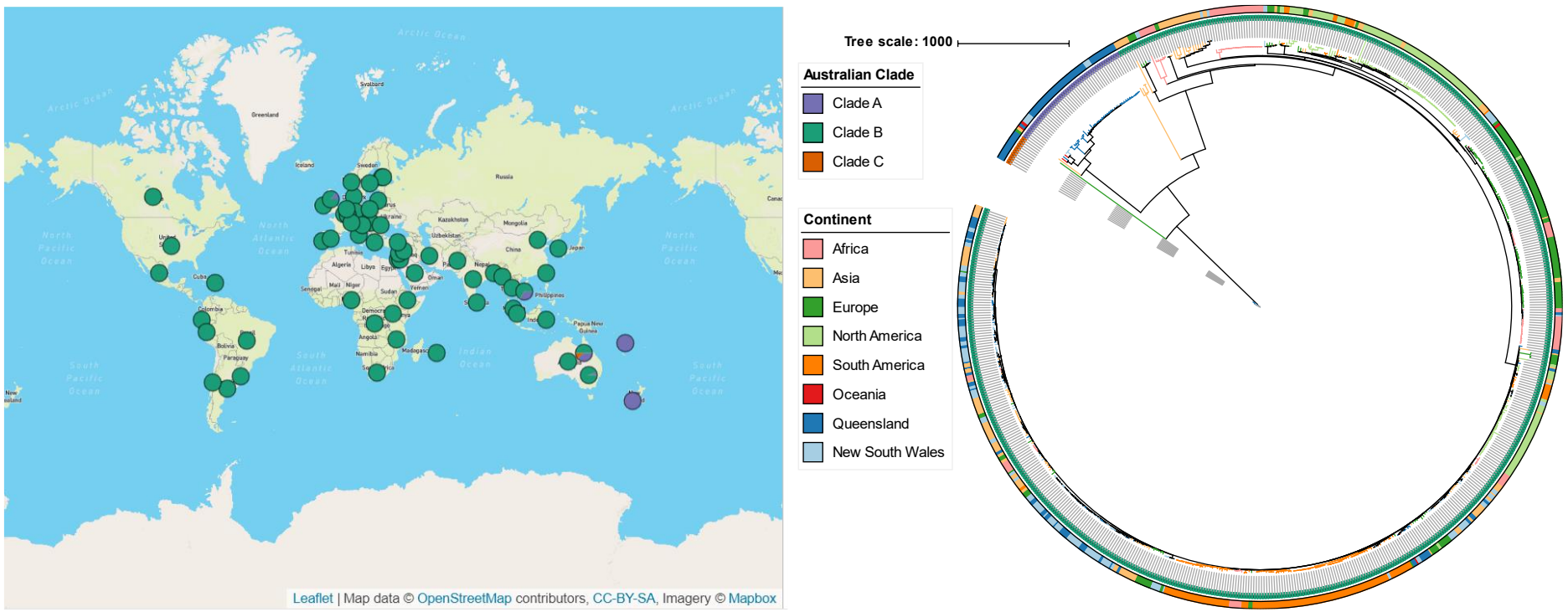


Figure 6.3: NJTree of the NSW isolates and global representatives. A NJTree was created using the cgMLST alleles. The NJTree consisted of 59 African isolates (light red), 100 Asian (light orange), 100 European (dark green), 100 North American (light green), 100 South American (dark orange), 6 Oceanian (dark red), 100 from Queensland (dark blue) and 95 from NSW (light blue).

Clade C consisted entirely of isolates from Queensland, while Clade A was comprised predominantly of Oceanian isolates, however one European (17549) and one Asian (17407) isolate were also present in Clade A. Clade B was composed of isolates from across the continents. African isolates were predominantly ancestral, although some were admixed with the European clade. North American isolates formed two distinct clades with little admixture. The South American isolates also formed a distinct clade with very little admixture. Asian isolates formed two clades, one of which was small and ancestral to the majority of Clade B isolates, the other Asian clade was highly admixed with the Oceanian isolates.

The Oceanian isolates (95 NSW, 191 Queensland and 6 Oceanian) were used in continent specific comparisons. These isolates were compared with 245 Asian, 229 European, 200 North American and 200 South American isolates (Figure 6.4). The highest degree of admixture was observed when the Oceanian isolates were compared with Asian isolates (Figure 6.4a). Clade B was highly admixed but could still be split into three specific lineages: An Asian lineage, an admixed lineage and an Australian lineage (microreact (Argimón *et al.*, 2016): https://microreact.org/project/BklGcpfbV). Comparisons with European serovar Enteritidis isolates split Clade B into a European and an Oceanian lineage the levels of admixture were still notable (Figure 6.4b) (microreact (Argimón *et al.*, 2016): https://microreact.org/project/BkH2Ppfb4). A comparison with North American serovar Enteritidis isolates split Clade B into four lineages with low levels of admixture, two were Oceanian and two were North American (Canada/USA and Mexico/USA) (Figure 6.4c) (microreact (Argimón *et al.*, 2016): https://microreact.org/project/Byp_D3MbV). The South American comparison split Clade B into an Oceanian and a South American lineage, which also had low levels of admixture between them (Figure 6.4d)

(microreact (Argimón *et al.*, 2016): https://microreact.org/project/Skg2S3GbV). The NJTrees were highly congruent with the minimum spanning trees produced using GrapeTree (Zhou *et al.*, 2018) (Appendix U).

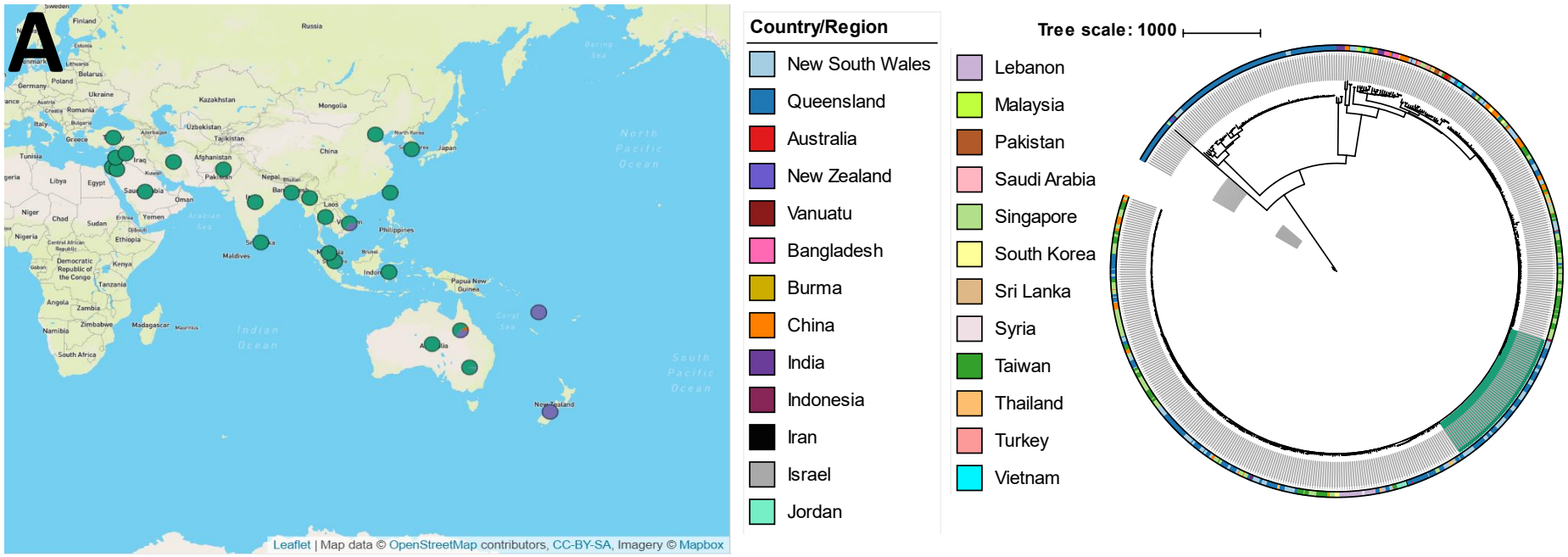


Figure 6.4: NJTrees of Oceanian isolates and global representatives from Asia (A), Europe (B), North America (C) and South America (D). The NJTrees were created using cgMLST alleles, all of the trees included the 95 NSW isolates, 191 Queensland isolates and 6 Oceanian isolates. The trees were annotated using country of isolation for all isolates and region for the Queensland and NSW isolates.

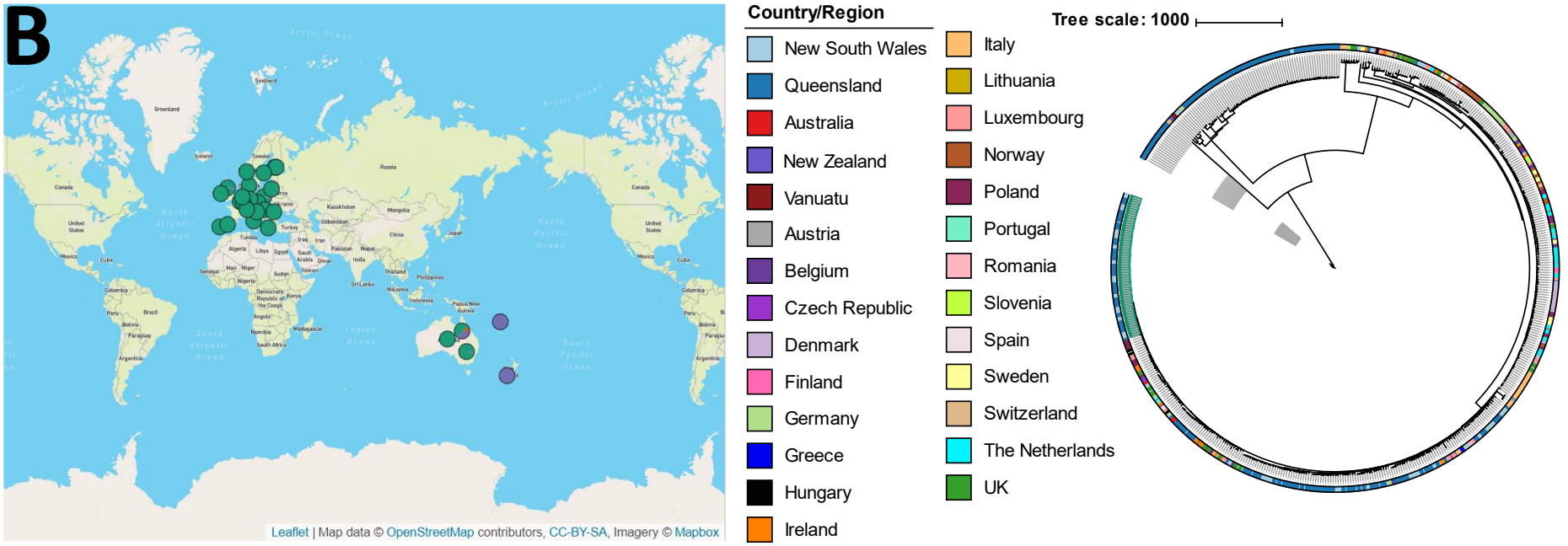


Figure 6.4: NJTrees of Oceanian isolates and global representatives from Asia (A), Europe (B), North America (C) and South America (D). The NJTrees were created using cgMLST alleles, all of the trees included the 95 NSW isolates, 191 Queensland isolates and 6 Oceanian isolates. The trees were annotated using country of isolation for all isolates and region for the Queensland and NSW isolates.

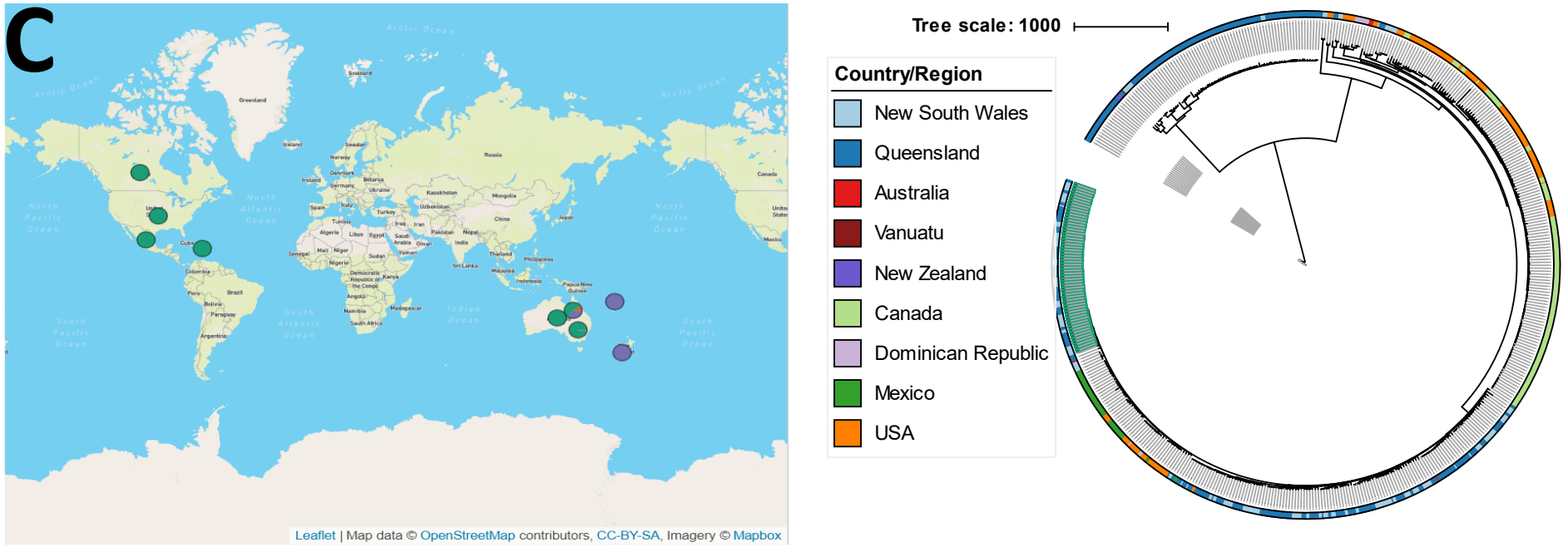


Figure 6.4: NJTrees of Oceanian isolates and global representatives from Asia (A), Europe (B), North America (C) and South America (D). The NJTrees were created using cgMLST alleles, all of the trees included the 95 NSW isolates, 191 Queensland isolates and 6 Oceanian isolates. The trees were annotated using country of isolation for all isolates and region for the Queensland and NSW isolates.

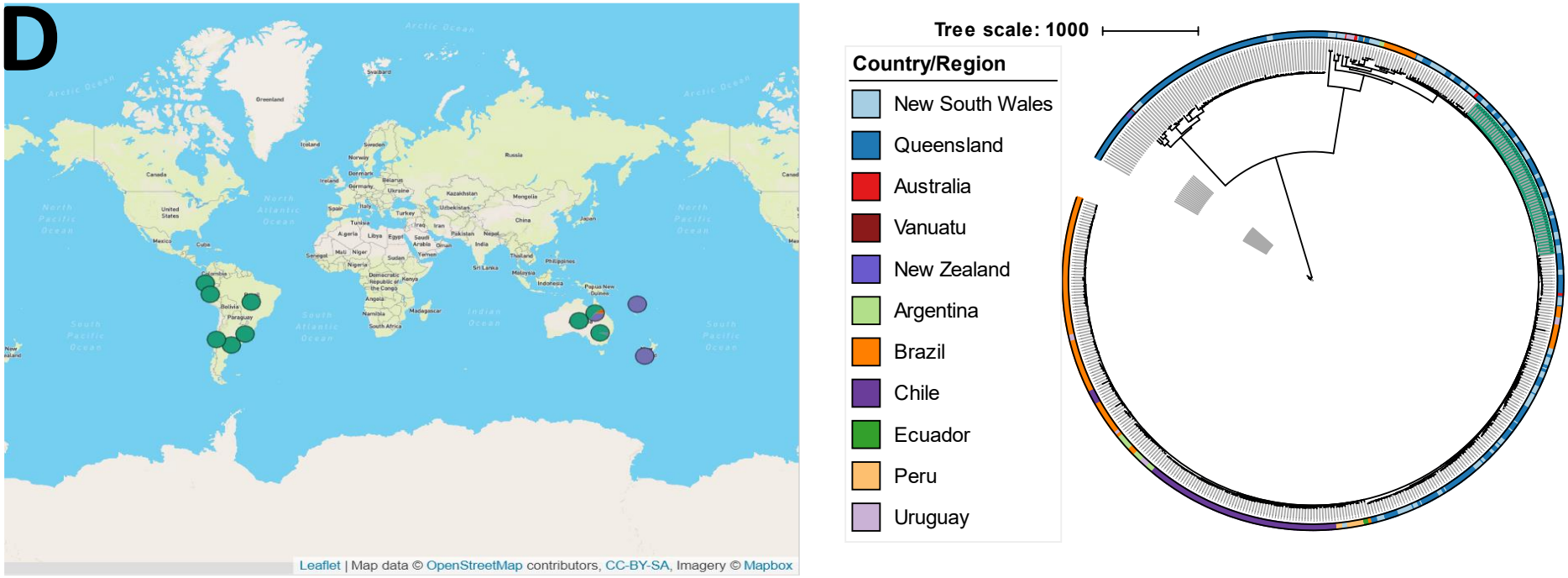


Figure 6.4: NJTrees of Oceanian isolates and global representatives from Asia (A), Europe (B), North America (C) and South America (D). The NJTrees were created using cgMLST alleles, all of the trees included the 95 NSW isolates, 191 Queensland isolates and 6 Oceanian isolates. The trees were annotated using country of isolation for all isolates and region for the Queensland and NSW isolates.

A: 245 Asian, 6 Oceanian, 95 NSW and 191 Queensland isolates were used to construct a NJtree. The Asian isolates consisted of up to 20 isolates per country or as many as were available, covering 20 Asian countries. The highest degree of admixture was observed in this comparison. Clade B was highly admixed but could still be split into three specific lineages: An Asian lineage, an admixed lineage and an Australian lineage. Many of the isolates were closely related, which is indicative of the import of serovar Enteritidis from Asia into Australia.

B: 229 European, 6 Oceanian, 95 NSW and 191 Queensland isolates were used to construct a NJtree. The European isolates consisted of up to 20 isolates per country or as many as were available, covering 22 European countries. Comparisons with European serovar Enteritidis isolates split the tree into a European and an Oceanian lineage but there were notable levels of admixture between the two clades, suggesting some transfer of serovar Entertidis between these two continents.

C: 200 North American, 6 Oceanian, 95 NSW and 191 Queensland isolates were used to construct a NJtree. The N. America isolates were from: Canada, Dominican Republic, Mexico and USA, with the majority of isolates coming from Canada or the USA. Four clades were observed, two were Oceanian and two were North American (Canada/USA and Mexico/USA). Isolates were not particularly admixed between Australia and North America, suggesting that North American and Australian isolates are not closely related.

D: 200 South American, 6 Oceanian, 95 NSW and 191 Queensland isolates were used to construct a NJtree. The South American isolates were from: Argentina, Brazil, Chile, Ecuador, Peru and Uruguay, with the majority of isolates coming from Brazil and Chile. Isolates fell into two separate clade, one South American and one Australian. These clades had very little admixture, with less than 20 South American isolates grouping with the Australian isolates.

A cluster of 57 isolates within Clade B were all from NSW or Queensland (Figure 6.5). These isolates also had low levels of acquired AMR genetic determinants, all isolates

had *aac(6')-Iaa* but only two isolates had further acquired AMR genes, isolate 17678 had acquired *aadA1* and *fosA4* and isolate 18109 had acquired bla_{TEM-1D}. All of the NSW isolates carried the *gyrA p.*D87N point mutation, while all but one isolate (18109). The remaining 26 isolates also had a mutation in the *gyrA* gene, all but one of which was *gyrA* p.D87N, the other was *gyrA* p.S83F. This cluster was also observable within the minimum spanning trees.

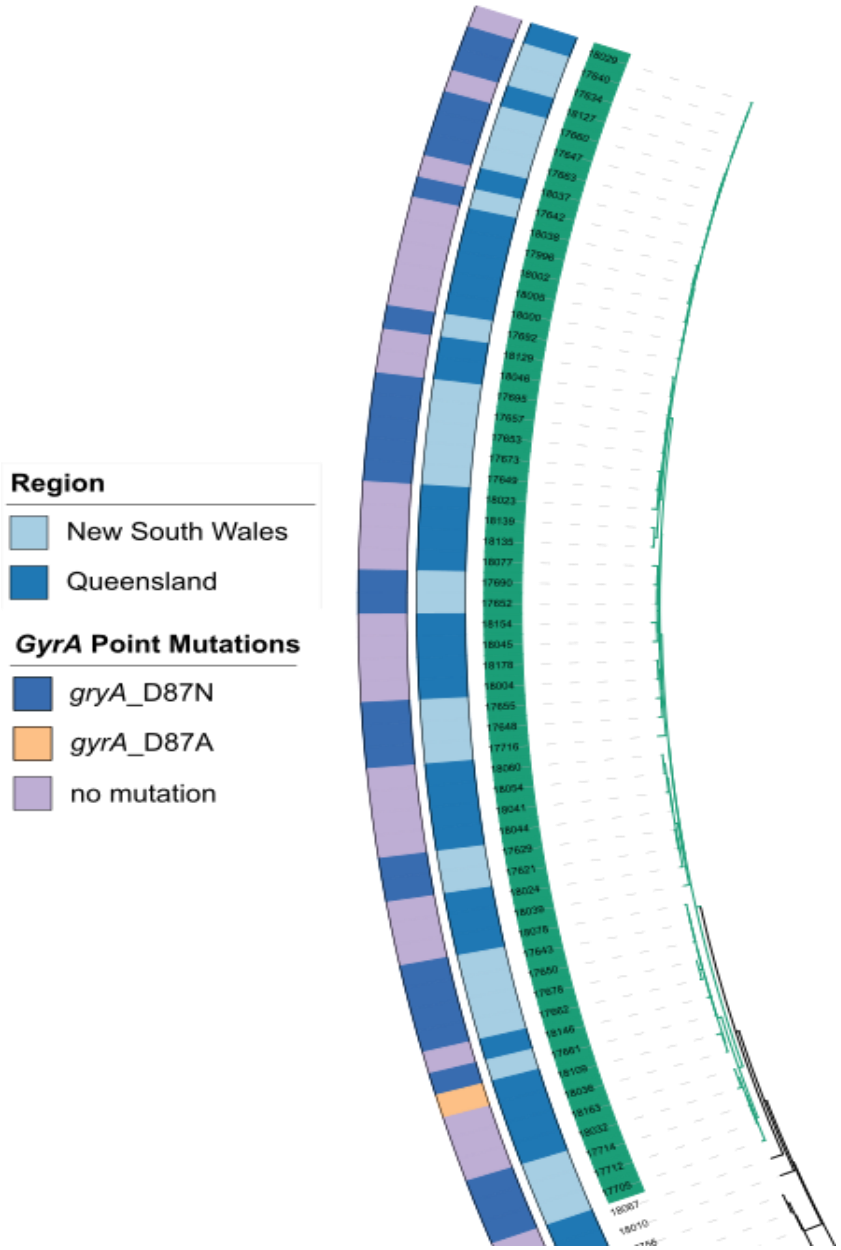


Figure 6.5: Australian lineage observed within comparisons with all of the continents. A region of Clade B within all of the NJtrees consisted of 57 isolates all from NSW and Queensland, which formed its own clade. These isolates carried low levels of resistance, 29 had only *aac(6')-Iaa* with no point mutations in *gyrA*. Isolate 17678 had acquired *aadA1* and *fosA4* and isolate 18109 had acquired $bla_{TEM\text{-}1D}$, these isolates also carried the *gyrA* p.D87N point mutation. The remaining isolates had a mutation in the *gyrA* gene, 25 had *gyrA* p.D87N, and one had *gyrA* p.S83F. This could represent an Australian lineage of Clade B.

6.4 Discussion

S. enterica serovar Enteritidis is a particularly homogenous non-host restricted serovar of *S. enterica* (Olson *et al.*, 2007; Allard *et al.*, 2013). The use of WGS-based approaches, such as SNP and cgMLST analysis are capable of fine typing isolates within this serovar (Deng *et al.*, 2014; Langridge *et al.*, 2015; Feasey *et al.*, 2016; Graham *et al.*, 2018). This has enabled the identification of multiple lineages within serovar Enteritidis that occupy different niches, for example geographical location (Feasey *et al.*, 2016) or host (Deng *et al.*, 2014); as well as enabling identification and analysis of serovar Enteritidis outbreaks (Dallman *et al.*, 2016). Within Queensland, Australia three clades of serovar Enteritidis had been identified: Clade A, B and C (Graham *et al.*, 2018). Clade B appeared to relate to a previously identified global clade (Deng *et al.*, 2014; Graham *et al.*, 2018), while Clades A and C appeared to be predominantly associated with infections that occur within Australia (Graham *et al.*, 2018).

In comparison, the analysis of serovar Enteritidis isolates from New South Wales, Australia only clustered within two of these clades – Clades A and B. This suggested that despite these isolates being identified within the same country the spread of serovar Enteritidis transmission within these states was different. Furthermore, the proportion of isolates belonging to each clade varied between the two states, of the 211 isolates analysed within the Queensland dataset 37% (78) belonged to Clade A (Graham *et al.*, 2018), in contrast only 5.3% (5) of the 95 NSW isolates belonged to Clade A. This could have been due to differences between the two states such as sources, hosts, individual interactions with environments and travel preferences etc.

Differences between the sources of isolates within the datasets could also have been a contributing factor (Graham *et al.*, 2018); in the Queensland dataset eleven isolates were from environmental sources, eight belonged to Clade A and three to Clade C (Graham *et al.*, 2018), whereas all of the isolates from NSW were clinical. While the presence of environmental isolates within the Queensland dataset could account for some of the differences between the proportions of isolates that belonged to each clade it was not enough to account for all of the differences between the two datasets, as even if the environmental isolates were removed from the Queensland dataset 70 out of 200 isolates (35%) still belonged to Clade A, which is still considerably larger than 5.3% of the NSW isolates.

The Clade A isolates in both Queensland and NSW were highly similar. As observed within the majority of Clade A isolates within the Queensland analysis (Graham *et al.*, 2018), all of the NSW Clade A isolates (17679, 17688,17706, 17710 and 17721), carried no acquired AMR genes or *gyrA* point mutations, except for the resistance determinant gene *aac(6')-Iaa*, which was present in all serovar Enteritidis isolates (Magnet, Courvalin and Lambert, 1999). The lack of AMR genes within these isolates was not consistent with the levels of resistance in serovar Enteritidis globally (Crump *et al.*, 2011; Hur *et al.*, 2011; Thong *et al.*, 2016). No Clade A isolates from NSW carried any plasmids, while four of the Clade A isolates in the Queensland dataset carried at least one plasmid. While the incidence of plasmids within the Clade A isolates was higher in the Queensland (Graham *et al.*, 2018) dataset than the NSW dataset, in both the Queensland (Graham *et al.*, 2018) and NSW datasets the incidence of plasmids was considerably higher in Clade B than it was in Clade A. As many AMR genes were plasmid acquired to protect against antimicrobials in their

environment (Bennett, 2008), the lack of AMR genes and plasmids within these isolates suggested that the Clade A isolates were not exposed to antimicrobials (Gullberg *et al.*, 2011) or were not exposed to plasmids. These isolates could also have been geographically restricted or host adapted and would therefore be unable to acquire AMR genes through plasmid transfer (Bennett, 2008) or horizontal gene transfer (Davies and Davies, 2010). It is possible that these isolates were not exposed to bacteria that carried an AMR-associated gene (Bennett, 2008; Davies and Davies, 2010) because they were circulating in a restricted niche with little exposure to other bacterial populations or antimicrobials. It is also possible that these isolates were not frequently exposed to antimicrobials, as carrying AMR determinants and/or plasmids has fitness costs (Carroll and Wong, 2018).

The analysis of SPIs within the two datasets (NSW and Queensland) were highly congruent (Graham *et al.*, 2018). With the exception of two Clade B isolates from the NSW dataset (17694 and 17703), in which the SPI-19 genes were also present. These isolates were very closely related to each other and were ancestral to the rest of Clade B, suggesting that they may represent a link between the two clades (Figure 6.2). Furthermore, two of the NSW Clade A isolates (17706 and 17710) also had nearly intact copies of SPI-21, unlike the Queensland isolates; suggesting that there are some differences in serovar Enteritidis between the two states.

Differences between the two Australian states are also supported by differences between the Clade B isolates within each of these datasets. Isolates within the NSW and Queensland (Graham *et al.*, 2018) datasets carried different AMR determinant

genes, for example streptomycin resistance determinants were only observed in the Queensland isolates (Graham *et al.*, 2018). The differences in acquired AMR genetic determinants are predominantly minor and could be explained due to differences in the programs used to detect the AMR genes (Zankari *et al.*, 2012; Graham *et al.*, 2018). In contrast, the same program (Zankari *et al.*, 2012) was used to detect point mutations within the *gyrA* gene and there were considerable differences between the two states, as considerably more NSW isolates carried point mutations and the type of mutations present varied considerably between the two states. There was clear biological variation between the two datasets, for instance, the differences in AMR genetic determinants; however, the reasons behind these differences remain unclear. For example, the variation may not have been due to geography but could have been due to temporal changes, if these samples were collected within different time periods then resistance levels and common point mutations may have changed through selection or stochastic effects (Davies and Davies, 2010; Gullberg *et al.*, 2011).

Placing all of the Oceanian isolates (NSW dataset, Queensland dataset, Australian isolates, one isolate from Vanuatu and one from New Zealand) in a global context (Figures 6.3) leant further support to the identification of Clade B as a global clade (Deng *et al.*, 2014). The vast majority of isolates from Africa, Asia, Europe, North America and South America that were used within this analysis clustered within Clade B. Only one isolate from Europe and one from Asia, from over 200 randomly selected isolates from each of these continents, were not located within Clade B.

The majority of Clade B consisted of very closely related isolates that initially appeared to have minimum genetic variation within phylogenies and the analysis of SPIs, AMR determinants etc. This was in keeping with previous findings that serovar Enteritidis was highly homogenous (Olson *et al.*, 2007; Allard *et al.*, 2013). When the isolates were labelled with their continent of origin, however, Clade B was resolved into broadly continent specific lineages (Figure 6.3). The Australian Clade B isolates predominantly clustered with isolates from Asia (Figure 6.3). This supported the findings that the majority of Australian serovar Enteritidis infections were imported from travel to Asia (OzFoodNet Working Group, 2015).

When all of the Oceanian isolates were compared to isolates from each continent separately there were considerable differences between the continents. Australian and Asian isolates were considerably more mixed within a single clade than Australian isolates and European, North American or South American isolates. North and South American isolates demonstrated very little admixture with Oceanian isolates, suggesting that import and export of serovar Enteritidis between these continents was uncommon. This many be because travel to South America by Australians is less common than the other continents (Australian Bureau of Statistics, 2018). The levels of admixture between European and Oceanian was higher, suggesting that there was some import of serovar Enteritidis strains from Europe into Australia. The highest degree of admixture was observed when the Oceanian isolates were compared with Asian isolates but Clade B could still be split into three specific lineages: An Asian lineage, an admixed lineage and an Australian lineage. The high degree of admixture with Asian isolates was not surprising as the majority of Australian travel is to Asia (Australian Bureau of Statistics, 2018) and previous traceback analyses have found

that the majority of reported serovar Enteritidis cases are associated with reports of recent travel to Asia (OzFoodNet Working Group, 2015).

Of particular interest though was the lineage of 57 Australian isolates that formed an Australia specific clade (Figure 6.4 and 6.5). While it is possible that increased sampling of Asian countries, especially those which are popular holiday destinations, such as Indonesia and Malaysia (OzFoodNet Working Group, 2015; Australian Bureau of Statistics, 2018) could demonstrate that this lineage was also Asian in origin. These isolates also had lower levels of AMR than expected (Crump *et al.*, 2011; Thong *et al.*, 2016). A characterisation of AMR within serovar Enteritidis from Malaysia demonstrated relatively high levels of nalidixic acid and ciprofloxacin resistance (Thong *et al.*, 2016), which was considerably different from the AMR profiles observed within the Australian lineage (Figure 6.5). All but two isolates had no acquired AMR genes except for *aac(6')-Iaa* (Magnet, Courvalin and Lambert, 1999), this was considerably lower than the levels of acquired AMR resistance that were circulating globally (Crump *et al.*, 2011; Hur *et al.*, 2011; Thong *et al.*, 2016). This suggested that these isolates were not being frequently exposed to antimicrobials (Davies and Davies, 2010; Gullberg *et al.*, 2011) and the population was potentially isolated from other serovar Enteritidis strains. This would have prevented the acquisition of AMR genes through plasmid transfer (Bennett, 2008) or horizontal gene transfer (Davies and Davies, 2010). Isolation could have been purely geographical (Boore *et al.*, 2015) or these isolates could also have been isolated due to being host restricted (Lawson *et al.*, 2018). Furthermore, when point mutations within the *gyrA* gene of the 57 isolates were analysed none of the Queensland isolates carried a mutation (Graham *et al.*, 2018), while all of the NSW isolates carried the D87N mutation, except for one which

carried D87A. This suggests that there was also a regional difference between the isolates within this Australian lineage and that the NSW isolates were exposed to quinolones and have therefore evolved or acquired increased resistance (Davies and Davies, 2010; Gullberg *et al.*, 2011), while the Queensland isolates were not exposed and therefore have remained susceptible. This lineage of 57 isolates was present in all of the continent comparisons and isolates within it always formed a distinct clade (Figure 6.4).

The presence of this Australian specific lineage within the global clade indicated that there may have been a more recent introduction of serovar Enteritidis into Australia and that this lineage has been persisting within the country. It was therefore possible that less cases of serovar Enteritidis are imported into Australia than had previously been believed and that some of the travel associated cases (OzFoodNet Working Group, 2015) may have been acquired within Australia. These isolates may have been persisting within the environment in a niche that was not exposed to antimicrobials as these isolates were predominantly susceptible to antimicrobials (Gullberg *et al.*, 2011).

Results from this study demonstrated that there were not only differences among the serovar Enteritidis isolates (AMR, pathogenicity etc.) found in Australia and the global populations but also within the isolates found within Australia. Between Queensland (Graham *et al.*, 2018) and NSW not only were there different proportions of the serovar Enteritidis clades circulating, there were also differences within the AMR determinant gene profiles. Most notably resistance to quinolones varied strongly between the two states. This suggests that a large-scale characterisation of serovar Enteritidis isolates

across Australia may be beneficial to monitor the prevalence of different strains and to characterise regional differences. Comparisons of Australian isolates with serovar Enteritidis isolates from across the globe supported previous findings that there is considerable import of serovar Enteritidis into Australia from Asia (OzFoodNet Working Group, 2015). Unlike previous analyses (Deng *et al.*, 2014; Graham *et al.*, 2018) though an Australian specific lineage was identified here within the global clade of Clade B. Further characterisation of isolates of serovar Enteritidis from Australia may identify further isolates that belong to this lineage and could also identify further regional differences.

6.5 Conclusions

Isolates of serovar Enteritidis from New South Wales were split into two of the three clades that were identified in an analysis of serovar Enteritidis isolates from Queensland. This, as well as differences in point mutation profiles within the *gyrA* gene, suggested that there were regional differences between serovar Enteritidis isolates identified within New South Wales and Queensland. Phylogenetic comparisons among all of the Oceanian isolates and global isolates identified that the Australian isolates were most closely related to isolates from Asia. This was consistent with previous findings that the majority of serovar Enteritidis cases within Australia had recently travelled to Asia. Further phylogenetic analyses did, however, reveal an Australian specific lineage within the global clade, which indicated a more recent import of serovar Enteritidis back into Australia. The low levels of AMR and the consistency of the AMR profiles associated with the Australian lineage within Clade B suggested that it was persisting within Australia and that it was not often exposed to antimicrobials. The collection of more isolates from popular holiday destinations such as Indonesia and Malaysia could help to further confirm if this lineage was truly Australian. The collection of detailed travel histories from the infected individuals could also help to confirm or deny this lineage. Furthermore, the collection of further Australian isolates from the other Australian states could identify more isolates which belonged to this lineage. Irrespective of the origin of this lineage, the differences between NSW and Queensland demonstrated that there were regional differences within serovar Enteritidis strains across Australia and an in-depth analysis would provide a clearer image of the situation across the country.

Statement of Authorship for joint/multi-authored papers for PGR thesis

To appear at the end of each thesis chapter submitted as an article/paper

The statement shall describe the candidate's and co-authors' independent research contributions in the thesis publications. For each publication there should exist a complete statement that is to be filled out and signed by the candidate and supervisor **(only required where there isn't already a statement of contribution within the paper itself).**

Title of Paper	A characterisation of *Salmonella enterica* serovar Enteritidis from New South Wales, Australia
Publication Status	Unpublished and unsubmitted, written in a manuscript style
Publication Details	M. Pearce, V. Sintchenko and M. Maiden

Student Confirmation

Student Name: Madison Pearce		
Performed all analysis, data interpretation, prepared manuscript for publication, constructed and edited all of the figures.		
Signature	Date	

Supervisor Confirmation

By signing the Statement of Authorship, you are certifying that the candidate made a substantial contribution to the publication, and that the description described above is accurate.

Supervisor name and title:		
Supervisor comments:		
Signature	Date	

Chapter Seven

Final Discussion

Globally *Salmonella* infections have the highest burden of disease of all infectious intestinal diseases (Kirk *et al.*, 2015). Non-typhoidal and serovar Typhi cases have the highest and second highest levels of burden when analysed using DALYs (Kirk *et al.*, 2015). Routine surveillance followed by investigation and characterisation of isolates in order to understand the molecular epidemiology of this genus is therefore necessary (Feasey *et al.*, 2012; Wong *et al.*, 2016). A greater understanding of the *Salmonella* can in turn inform novel approaches which may be able to significantly reduce the burden of disease (Feasey *et al.*, 2012; Wong *et al.*, 2016). Novel approaches such as more effective vaccines against serovar Typhi (Martin, 2012) and the introduction of vaccines against Paratyphi A (Martin, 2012) or invasive non-typhoidal *Salmonella* (Haselbeck *et al.*, 2017) infections could help reduce the burden of disease (MacLennan, Martin and Micoli, 2014). Improved monitoring and reporting of *Salmonella* globally could also aid in the reduction of disease burden, as outbreaks may be detected earlier (den Bakker *et al.*, 2011; Hoffmann *et al.*, 2016; Phillips *et al.*, 2016; Waldram *et al.*, 2018), allowing for earlier interventions. Furthermore, a better knowledge of AMR profiles associated with specific countries or sources may also help to inform more rapid and targeted treatment of an infection (Wong *et al.*, 2016; Carroll *et al.*, 2017).

Using conventional methods serotyping can be performed in approximately one hour (APHL, 2014); however, if an isolate requires additional work to enhance motility and

flagellar antigenic expression or antisera is unavailable at the time of analysis the amount of time taken can rise considerably (APHL, 2014). AMR detection using conventional disk-based diffusion approaches can take between 18 – 24 hours (Jorgensen *et al.*, 2009) and the characterisation of virulence genes varied greatly but can take over 96 hours when incubation times were also taken into consideration (Shomer *et al.*, 2016). In-depth characterisation of a single isolate was time-consuming when using conventional methods (Jorgensen *et al.*, 2009; APHL, 2014; Shomer *et al.*, 2016), therefore it was not feasible for these tests to be performed as part of a routine analysis. WGS can be used as a 'one-stop' shop (Moran-Gilad, 2017) and all of these tests can be performed routinely following sequencing and assembly of an isolate (Moran-Gilad, 2017), which can be used to improve the understanding of the molecular epidemiology within *Salmonella.* This increased knowledge on the characteristics of individual isolates can also be scaled up to populations (Cao *et al.*, 2013; Graham *et al.*, 2018) and even applied globally (Deng *et al.*, 2014; Kuijpers *et al.*, 2016), enabling better monitoring and reporting of *Salmonella* disease. The primary aim of this thesis was to determine the utility of WGS within the analysis of *Salmonella* and demonstrate the public health impacts.

The most common method for *Salmonella* outbreak analysis when using WGS is currently SNP-based typing (den Bakker *et al.*, 2011; Ashton *et al.*, 2016; Loman *et al.*, 2016). SNP analysis has several limitations though, the use of different pipelines and references can impact the results of outbreak investigations (Gymoese *et al.*, 2017; Saltykova *et al.*, 2018). For instance, the distances between isolates can be altered (Saltykova *et al.*, 2018) and this can make the analysis of outbreaks across borders difficult. In the second chapter of this thesis SNP typing was compared with

cgMLST. A multi-country outbreak of serovar Enteritidis was used in order to determine the ability of cgMLST to identify and characterise outbreak isolates. This analysis demonstrated that cgMLST and SNP-based typing were highly congruent and that cgMLST could be used within outbreak investigations as effectively as SNPs. There are advantages to using cgMLST over SNP-based typing though, cgMLST is reference free and can be applied to any isolate that is covered by the scheme, removing the need to create different schemes for every serovar. Furthermore, cgMLST is easily transportable across borders as it can be made available via online databases. It is most likely because of these advantages that PulseNet has identified cgMLST as the replacement for pulsed-field gel electrophoresis (PFGE) for the communication of gastrointestinal outbreak strains (Nadon *et al.*, 2017).

An accurate cgMLST scheme for the identification and investigation of non-subspecies I isolates is also necessary. While the majority of *Salmonella* infections are caused by subspecies I, the non-subspecies I *Salmonella* are opportunistic pathogens (Lamas *et al.*, 2018) and infection with these isolates can still lead to complications (Mukai, Agatsuma and Ideura, 2018) and death (Mahajan *et al.*, 2003). Despite the findings that the Enterobase cgMLST scheme (EBcgMLST) was able to accurately characterise subspecies I outbreaks and was comparable with SNP-based typing approaches in chapter two, the EBcgMLST scheme had not been systematically assessed for its performance at the genus level. This was therefore the focus of chapter three of this thesis. Analysis showed, however, that the relationships among the *Salmonella enterica (S. enterica)* subspecies and *Salmonella bongori (S. bongori)* were misrepresented when EBcgMLST was utilised. Further examination identified 252 loci that did not meet the inclusion criteria for a core scheme when the *S. enterica*

subspecies and *S. bongori* were analysed individually. Therefore, these 252 loci were removed for the creation of a core genus scheme (SalmcgMLST). This scheme more accurately reflected the relationships across the genus (McQuiston *et al.*, 2008; Alikhan *et al.*, 2018) when compared with the EBcgMLST scheme and is proposed for genus wide analyses within the salmonellae. The EBcgMLST scheme is, however, accurate for subspecies I investigations and the increased resolution granted by this scheme should continue to be utilised for investigations that are subspecies I specific.

The SalmcgMLST scheme was then used for a large-scale analysis of the *Salmonella* genus in chapter four. Non-subspecies I *Salmonella* have often been neglected, as they are not responsible for the majority of human disease (CDC, 2008). This analysis identified a novel subspecies that had previously gone uncharacterised. All of the conventionally and phylogenetically identified species and subspecies were genetically distinct (Boyd *et al.*, 1996; Grimont and Weill, 2007; Alikhan *et al.*, 2018), even though biochemical approaches could not distinguish between all of these groups (Boyd *et al.*, 1996; Grimont and Weill, 2007). Furthermore, the results also suggested that subspecies IIIa isolates were ancestral to the other *S. enterica* subspecies and supported the reclassification of subspecies IIIa as a separate species – *Salmonella arizonae (S. arizonae*). This analysis demonstrated that rMLST (Jolley *et al.*, 2012) can be used for the identification of subspecies from WGS. As public health laboratories are increasingly adopting WGS for routine surveillance (Ashton *et al.*, 2016) this analysis can have real world impacts for the identification of species and subspecies directly from the sequence. Furthermore, public health facilities will be able to accurately report all of the *Salmonella* species and subspecies.

The final chapter of this thesis looked to examine the uses of WGS beyond the identification and clustering of *Salmonella* isolates for routine reporting or outbreak investigation. Therefore, an analysis focusing on the characterisation and the phylogeography of *S. enterica* serovar Enteritidis in NSW, Australia was undertaken. Within this analysis WGS was used to characterise a dataset of 95 serovar Enteritidis isolates from NSW and these were compared with other Australian isolates (Graham *et al.*, 2018) and serovar Enteritidis isolates from across the globe. From the WGS it was possible to characterise AMR genes (Zankari *et al.*, 2012), plasmids (Carattoli *et al.*, 2014) and pathogenicity islands as well as comparing the relationships among serovar Enteritidis isolates globally through the use of phylogenetic analyses. The combination of phylogenetics with AMR profiles, plasmids and SPI-islands was able to demonstrate differences in the spread of serovar Enteritidis within Australia and globally. Phylogenetic analyses revealed strong associations with isolates from Asia, which supported previous conclusions (OzFoodNet Working Group, 2015) that the majority of serovar Enteritidis cases are imported into Australia following travel to Asia (OzFoodNet Working Group, 2015). This analysis did, however, also identify Australian specific lineages (Graham *et al.*, 2018), including one which could represent a more recent introduction of serovar Enteritidis into the country that has since persisted within the country. This analysis demonstrated the utility of WGS for the analysis of geographically related isolates and the results of analyses such as this one could be used to inform public health interventions. For example, through informing the general public of the risk associated with travel and steps that can be undertaken to reduce these risks.

The research conducted throughout this thesis made particular use of the MLST approach (Maiden *et al.*, 1998). The MLST approach can be upscaled to fit the needs of the analysis being performed (Maiden *et al.*, 2013). To identify and cluster *Salmonella* isolates into groups such as species and subspecies MLST or rMLST (Jolley, Bliss, *et al.*, 2012) can be utilised, as was demonstrated here in Chapter Five. The rMLST loci are of particular use for the analysis of isolates from across the whole of bacterial life as these loci are conserved across bacterial species (Jolley, Bliss, *et al.*, 2012) and therefore enable the clustering of isolates from across the prokaryotic domain. For more in-depth analyses of isolates the MLST approach can be further upscaled to cgMLST or wgMLST. These approaches can be used for the analyses of *Salmonella* outbreaks and were highly congruent to SNP-based approaches, as was demonstrated in Chapter Three. Additionally, cgMLST had the added benefits over SNP-based approaches of being stable, reference-free and easily communicable across borders using online databases. Using cgMLST it was also possible to investigate the phylogeography, AMR determinants and virulence genes of *Salmonella*, as was done in Chapter Six. Caution must, however, be taken when developing and choosing schemes, as was demonstrated in Chapter Four. If schemes aren't developed using the correct datasets or if the wrong scheme is used to analyse a dataset then incorrect results can occur. For example, in Chapter Four the relationships between *Salmonella* subspecies were incorrectly represented when isolates were analysed with the EBcgMLSTv2.0 scheme. Finally, the scheme can be upscaled to use the entirety of the genome sequence, this was demonstrated within this thesis in Chater Five for the confirmation of *Salmonella* species and subspecies. These schemes have enabled the analyses undertaken throughout this thesis and will have considerable benefits within public health setting.

This thesis provides clear evidence that WGS can become a ‘one-stop’ shop (Moran-Gilad, 2017) solution to the routine identification, investigation and characterisation of *Salmonella*. The decreasing costs of sequencing technology will allow more laboratories to make this transition (Moran-Gilad, 2017) and enable the establishment of systems that can monitor *Salmonella*, as well as genes of interest, potentially on a global scale. A rate limiting step is that the analysis of WGS can require significant bioinformatic expertise; however, this can be mitigated through the use of online tools (Zankari *et al.*, 2012; Carattoli *et al.*, 2014) and databases (Jolley and Maiden, 2010) that are easy to access and implement with a minimal degree of technical understanding (Jolley and Maiden, 2010). There is still a considerable degree of work to be done though, for example the development of a standardised clustering system to enable the clustering of cgMLST profiles into related groups. The development of such a scheme would make the communication of outbreak strains considerably simpler. While the characterisation of further serovar Enteritidis isolates from across Australia would further the understanding of the spread of this serovar across the separate regions of the country. Further isolates that belong to the novel Australian lineage could be identified, providing further support for the more recent introduction of serovar Enteritidis into the country and the persistence of this lineage within the environment. For this reason, all of the datasets created in this thesis will be made publicly available and publication in peer-reviewed journals will be sought for each of the chapters.

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Appendices

Appendix A

Additional data for the 535 *Salmonella* serovar Enteritidis isolates involved in the PT14b outbreak and used in Chapter Three

Uber strain	Name	Accession number	Collection Year	Collection Month	Collection Day	Continent	Country	Serovar	ST	SNP Addresses	dataset A	dataset B	dataset C
SAL_CA4860AA	34199	SRR1965044	2014	7	24	Europe	United Kingdom	Enteritidis	2066	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA4812AA	40793	SRR1965094	2014	8	12	Europe	United Kingdom	Enteritidis	2620 6	1.2.3.38.38.38.395	✓	✓	✓
SAL_CA4740AA	40799	SRR1965168	2014	8	15	Europe	United Kingdom	Enteritidis	2627 0	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA4651AA	25341	SRR1965266	2014	6	25	Europe	United Kingdom	Enteritidis	2634 7	1.2.3.38.38.38.38	✓	✓	✓
SAL_CA4566AA	50361	SRR1965353	2014	9	4	Europe	United Kingdom	Enteritidis	2066	1.2.3.38.38.38.413	✓	✓	✓
SAL_CA4560AA	38361	SRR1965359	2014	7	28	Europe	United Kingdom	Enteritidis	2066	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA4550AA	38314	SRR1965369	2014	7	29	Europe	United Kingdom	Enteritidis	2643 8	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA4544AA	32523	SRR1965375	2014	7	15	Europe	United Kingdom	Enteritidis	7153	1.2.3.38.38.38.393	✓	✓	✓
SAL_CA4510AA	38420	SRR1965410	2014	7	29	Europe	United Kingdom	Enteritidis	2646 8	1.2.3.38.38.38.413	✓	✓	✓
SAL_CA4496AA	37823	SRR1965424	2014	7	30	Europe	United	Enteritidis	264	1.2.3.38.38.38.393	✓	✓	✓

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SAL_CA4462AA	38418	SRR19654582	2014	7	30	Europe	United King dom	Enterit idis	26511	1.2.3.38.38.38.413	✓	✓	✓
SAL_CA4457AA	38311	SRR19654642	2014	7	29	Europe	United King dom	Enterit idis	26516	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA4417AA	37832	SRR19655062	2014	7	31	Europe	United King dom	Enterit idis	26550	1.2.3.38.38.38.2451	✓	✓	✓
SAL_CA4391AA	37819	SRR19655332	2014	7	29	Europe	United King dom	Enterit idis	20666	1.2.3.38.38.38.413	✓	✓	✓
SAL_CA4375AA	21777	SRR19655492	2014	6	12	Europe	United King dom	Enterit idis	26585	1.2.3.38.38.38.38	✓	✓	✓
SAL_CA4343AA	38766	SRR19655902	2014	8	5	Europe	United King dom	Enterit idis	20666	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA4339AA	38426	SRR19655962	2014	7	28	Europe	United King dom	Enterit idis	26616	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA4312AA	38421	SRR19656232	2014	7	29	Europe	United King dom	Enterit idis	26639	1.2.3.38.38.38.413	✓	✓	✓
SAL_CA4259AA	31929	SRR19656792	2014	7	21	Europe	United King dom	Enterit idis	26685	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA4247AA	38425	SRR19656922	2014	7	29	Europe	United King dom	Enterit idis	26696	1.2.3.38.38.38.1072	✓	✓	✓
SAL_CA4240AA	37828	SRR19657002	2014	7	28	Europe	United King dom	Enterit idis	26702	1.2.3.38.38.38.367	✓	✓	✓

SAL_CA4176AA	36522	SRR1965772	2014	7	23	Europe	United Kingdom	Enteritidis	267571.2.3.38.38.38.2621	✓	✓	✓
SAL_CA4151AA	37808	SRR1965800	2014	7	31	Europe	United Kingdom	Enteritidis	761121.2.3.38.38.38.367	✓	✓	✓
SAL_CA4000AA	34176	SRR1965958	2014	7	21	Europe	United Kingdom	Enteritidis	269091.2.3.38.38.38.393	✓	✓	✓
SAL_CA3971AA	31976	SRR1965987	2014	7	23	Europe	United Kingdom	Enteritidis	269361.2.3.38.38.38.393	✓	✓	✓
SAL_CA3877AA	32462	SRR1966087	2014	7	15	Europe	United Kingdom	Enteritidis	270201.2.3.38.38.38.367	✓	✓	✓
SAL_CA3860AA	31973	SRR1966105	2014	7	22	Europe	United Kingdom	Enteritidis	270361.2.3.38.38.38.393	✓	✓	✓
SAL_CA3836AA	37831	SRR1966129	2014	7	30	Europe	United Kingdom	Enteritidis	270571.2.3.38.38.38.367	✓	✓	✓
SAL_CA3814AA	31967	SRR1966151	2014	7	26	Europe	United Kingdom	Enteritidis	206661.2.3.38.38.38.367	✓	✓	✓
SAL_CA3772AA	39453	SRR1966194	2014	7	29	Europe	United Kingdom	Enteritidis	271081.2.3.38.38.38.367	✓	✓	✓
SAL_CA3742AA	46580	SRR1966225	2014	7	17	Europe	United Kingdom	Enteritidis	271371.2.3.38.38.38.367	✓	✓	✓
SAL_CA3727AA	31980	SRR1966240	2014	7	25	Europe	United Kingdom	Enteritidis	206661.2.3.38.38.38.367	✓	✓	✓
SAL_CA3628AA	34178	SRR1966339	2014	7	17	Europe	United Kingdom	Enteritidis	266229.2.3.38.38.38.393	✓	✓	✓

SAL_CA3618AA	36521	SRR1966349	2014	7	24	Europe	United Kingdom	Enteritidis	761 2	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA3584AA	46585	SRR1966383	2014	7	18	Europe	United Kingdom	Enteritidis	2728 3	1.2.3.38.38.38.393	✓	✓	✓
SAL_CA3580AA	31928	SRR1966387	2014	7	21	Europe	United Kingdom	Enteritidis	2728 7	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA3518AA	21778	SRR1966448	2014	6	12	Europe	United Kingdom	Enteritidis	674	1.2.3.38.38.38.38	✓	✓	✓
SAL_CA3488AA	68909	SRR1966478	2014	6	24	Europe	United Kingdom	Enteritidis	2737 1	1.2.3.38.38.38.38	✓	✓	✓
SAL_CA3480AA	38318	SRR1966486	2014	7	28	Europe	United Kingdom	Enteritidis	2737 9	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA3459AA	37812	SRR1966507	2014	7	31	Europe	United Kingdom	Enteritidis	2739 9	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA3413AA	31922	SRR1966554	2014	7	21	Europe	United Kingdom	Enteritidis	761 2	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA3385AA	23473	SRR1966582	2014	6	13	Europe	United Kingdom	Enteritidis	2745 9	1.2.3.38.38.38.1116	✓	✓	✓
SAL_CA3363AA	36498	SRR1966605	2014	7	28	Europe	United Kingdom	Enteritidis	2747 6	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA3279AA	39455	SRR1966692	2014	7	30	Europe	United Kingdom	Enteritidis	2755 2	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA3247AA	34194	SRR1966724	2014	7	24	Europe	United Kingdom	Enteritidis	7153	1.2.3.38.38.38.393	✓	✓	✓

SAL_CA3216AA	38316	SRR1966755	2014	7	28	Europe	United Kingdom	Enteritidis	27608	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA3141AA	32459	SRR1966830	2014	7	17	Europe	United Kingdom	Enteritidis	20668	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA3120AA	34189	SRR1966851	2014	7	25	Europe	United Kingdom	Enteritidis	27688	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA3048AA	37833	SRR1966923	2014	7	30	Europe	United Kingdom	Enteritidis	27750	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA3034AA	36525	SRR1966937	2014	7	24	Europe	United Kingdom	Enteritidis	27763	1.2.3.38.38.38.393	✓	✓	✓
SAL_CA3002AA	38313	SRR1966969	2014	7	28	Europe	United Kingdom	Enteritidis	27792	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA3000AA	38319	SRR1966971	2014	7	28	Europe	United Kingdom	Enteritidis	27794	1.2.3.38.38.38.393	✓	✓	✓
SAL_CA2969AA	36501	SRR1967002	2014	7	17	Europe	United Kingdom	Enteritidis	27822	1.2.3.38.38.38.393	✓	✓	✓
SAL_CA2943AA	38419	SRR1967028	2014	7	29	Europe	United Kingdom	Enteritidis	27844	1.2.3.38.38.38.413	✓	✓	✓
SAL_CA2932AA	46591	SRR1967039	2014	7	18	Europe	United Kingdom	Enteritidis	27852	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2891AA	34186	SRR1967080	2014	7	25	Europe	United Kingdom	Enteritidis	20668	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2886AA	32472	SRR1967085	2014	7	18	Europe	United Kingdom	Enteritidis	20668	1.2.3.38.38.38.367	✓	✓	✓

SAL_CA2882AA	36524	SRR1967089	2014	7	22	Europe	United Kingdom	Enteritidis	27888	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2872AA	21776	SRR1967099	2014	6	3	Europe	United Kingdom	Enteritidis	27897	1.2.3.38.38.38.38	✓	✓	✓
SAL_CA2811AA	23472	SRR1967160	2014	6	13	Europe	United Kingdom	Enteritidis	27950	1.2.3.38.38.38.38	✓	✓	✓
SAL_CA2801AA	37807	SRR1967170	2014	7	28	Europe	United Kingdom	Enteritidis	27959	1.2.3.38.38.38.2542	✓	✓	✓
SAL_CA2797AA	34185	SRR1967174	2014	7	22	Europe	United Kingdom	Enteritidis	71553	1.2.3.38.38.38.393	✓	✓	✓
SAL_CA2792AA	39450	SRR1967179	2014	7	23	Europe	United Kingdom	Enteritidis	27967	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2786AA	34196	SRR1967185	2014	7	25	Europe	United Kingdom	Enteritidis	27973	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2743AA	21770	SRR1967228	2014	6	6	Europe	United Kingdom	Enteritidis	67474	1.2.3.38.38.38.38	✓	✓	✓
SAL_CA2688AA	24040	SRR1967283	2014	6	20	Europe	United Kingdom	Enteritidis	28055	1.2.3.38.38.38.604	✓	✓	✓
SAL_CA2685AA	34197	SRR1967286	2014	7	24	Europe	United Kingdom	Enteritidis	20066	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2664AA	24986	SRR1967307	2014	6	28	Europe	United Kingdom	Enteritidis	28076	1.2.3.38.38.38.472	✓	✓	✓
SAL_CA2593AA	38317	SRR1967378	2014	7	28	Europe	United Kingdom	Enteritidis	28141	1.2.3.38.38.38.367	✓	✓	✓

SAL_CA2588AA	34184	SRR1967383	2014	7	22	Europe	United Kingdom	Enteritidis	28146	1.2.3.38.38.38.393	✓	✓	✓
SAL_CA2509AA	32463	SRR1967462	2014	7	17	Europe	United Kingdom	Enteritidis	28214	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2492AA	37809	SRR1967479	2014	7	29	Europe	United Kingdom	Enteritidis	76122	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2423AA	31923	SRR1967548	2014	7	23	Europe	United Kingdom	Enteritidis	28289	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2371AA	46589	SRR1967600	2014	7	17	Europe	United Kingdom	Enteritidis	28335	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2362AA	36464	SRR1967609	2014	7	25	Europe	United Kingdom	Enteritidis	20066	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2205AA	38371	SRR1967766	2014	7	28	Europe	United Kingdom	Enteritidis	28478	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2200AA	36526	SRR1967771	2014	7	28	Europe	United Kingdom	Enteritidis	20066	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2199AA	36531	SRR1967772	2014	7	29	Europe	United Kingdom	Enteritidis	28483	1.2.3.38.38.38.2321	✓	✓	✓
SAL_CA2191AA	24038	SRR1967780	2014	6	23	Europe	United Kingdom	Enteritidis	28491	1.2.3.38.38.38.472	✓	✓	✓
SAL_CA2184AA	31974	SRR1967787	2014	7	25	Europe	United Kingdom	Enteritidis	28497	1.2.3.38.38.38.393	✓	✓	✓
SAL_CA2113AA	31968	SRR1967858	2014	7	26	Europe	United Kingdom	Enteritidis	28559	1.2.3.38.38.38.367	✓	✓	✓

SAL_CA2084AA	38332	SRR1967887	2014	7	25	Europe	United Kingdom	Enteritidis	20666	1.2.3.38.38.38.1809	✓	✓	✓
SAL_CA1889AA	32466	SRR1967989	2014	7	18	Europe	United Kingdom	Enteritidis	28675	1.2.3.38.38.38.393	✓	✓	✓
SAL_CA1784AA	37810	SRR1968043	2014	7	29	Europe	United Kingdom	Enteritidis	28721	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA1771AA	38417	SRR1968051	2014	7	28	Europe	United Kingdom	Enteritidis	28729	1.2.3.38.38.38.413	✓	✓	✓
SAL_CA1654AA	37827	SRR1968120	2014	7	24	Europe	United Kingdom	Enteritidis	28815	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA1478AA	31917	SRR1968213	2014	7	18	Europe	United Kingdom	Enteritidis	28978	1.2.3.38.38.38.668	✓	✓	✓
SAL_CA1253AA	46590	SRR1968332	2014	7	17	Europe	United Kingdom	Enteritidis	29082	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA1071AA	46579	SRR1968486	2014	7	17	Europe	United Kingdom	Enteritidis	29224	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA0907AA	40235	SRR1968516	2014	8	12	Europe	United Kingdom	Enteritidis	29251	1.2.3.38.38.38.413	✓	✓	✓
SAL_CA0885AA	37817	SRR1968529	2014	7	26	Europe	United Kingdom	Enteritidis	27851	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA0837AA	37825	SRR1968556	2014	7	28	Europe	United Kingdom	Enteritidis	29305	1.2.3.38.38.38.808	✓	✓	✓
SAL_CA0821AA	31972	SRR1968564	2014	7	25	Europe	United	Enteritidis	20	1.2.3.38.38.38.367	✓	✓	✓

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SAL_CA0770AA	38422	SRR1968589	2014	7	25	Europe	United King dom	Enterit idis	2936	1.2.3.38.38.38.413	✓	✓	✓
SAL_CA0763AA	34188	SRR1968592	2014	7	25	Europe	United King dom	Enterit idis	2936	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA0694AA	37813	SRR1968627	2014	7	31	Europe	United King dom	Enterit idis	2943	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA0644AA	38344	SRR1968654	2014	7	28	Europe	United King dom	Enterit idis	2622	1.2.3.38.38.38.393	✓	✓	✓
SAL_CA0472AA	31966	SRR1968746	2014	7	25	Europe	United King dom	Enterit idis	2961	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA0378AA	37811	SRR1968796	2014	7	28	Europe	United King dom	Enterit idis	2969	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA0306AA	38325	SRR1968832	2014	7	30	Europe	United King dom	Enterit idis	2975	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA0244AA	23462	SRR1968861	2014	6	10	Europe	United King dom	Enterit idis	2981	1.2.3.38.38.38.38	✓	✓	✓
SAL_CA0199AA	41984	SRR1968882	2014	8	14	Europe	United King dom	Enterit idis	2983	1.2.3.38.38.38.2248	✓	✓	✓
SAL_CA0163AA	34175	SRR1968899	2014	7	22	Europe	United King dom	Enterit idis	2986	1.2.3.38.38.38.537	✓	✓	✓
SAL_CA0150AA	34177	SRR1968906	2014	7	22	Europe	United King dom	Enterit idis	7153	1.2.3.38.38.38.393	✓	✓	✓

SAL_CA0106AA	38369	SRR1968929	2014	7	30	Europe	United Kingdom	Enteritidis	299051	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA9962AA	32471	SRR1969002	2014	7	20	Europe	United Kingdom	Enteritidis	300222	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA9960AA	23493	SRR1969003	2014	6	19	Europe	United Kingdom	Enteritidis	300244	1.2.3.38.38.38.38	✓	✓	✓
SAL_BA9938AA	24039	SRR1969015	2014	6	23	Europe	United Kingdom	Enteritidis	300043	1.2.3.38.38.38.472	✓	✓	✓
SAL_BA9923AA	36395	SRR1969024	2014	8	3	Europe	United Kingdom	Enteritidis	300555	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA9834AA	46586	SRR1969069	2014	7	14	Europe	United Kingdom	Enteritidis	301125	1.2.3.38.38.38.393	✓	✓	✓
SAL_BA9822AA	34181	SRR1969076	2014	7	22	Europe	United Kingdom	Enteritidis	301335	1.2.3.38.38.38.393	✓	✓	✓
SAL_BA9738AA	36518	SRR1969134	2014	7	23	Europe	United Kingdom	Enteritidis	206606	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA9594AA	34179	SRR1969206	2014	7	21	Europe	United Kingdom	Enteritidis	303006	1.2.3.38.38.38.393	✓	✓	✓
SAL_BA9466AA	39452	SRR1969276	2014	7	28	Europe	United Kingdom	Enteritidis	304009	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA9440AA	38315	SRR1969298	2014	7	28	Europe	United Kingdom	Enteritidis	299305	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA9436AA	37798	SRR1969301	2014	7	28	Europe	United	Enteritidis	30004	1.2.3.38.38.38.367	✓	✓	✓

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SAL_BA9403AA	39454	SRR1969334	2014	7	28	Europe	United King dom	Enteritidis	2066	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA9397AA	26641	SRR1969340	2014	6	26	Europe	United King dom	Enteritidis	26971	1.2.3.38.38.38.472	✓	✓	✓
SAL_BA9388AA	27771	SRR1969349	2014	6	26	Europe	United King dom	Enteritidis	30473	1.2.3.38.38.38.472	✓	✓	✓
SAL_BA9365AA	46583	SRR1969372	2014	7	14	Europe	United King dom	Enteritidis	30496	1.2.3.38.38.38.393	✓	✓	✓
SAL_BA9337AA	37834	SRR1969400	2014	7	31	Europe	United King dom	Enteritidis	30520	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA9321AA	38779	SRR1969416	2014	8	7	Europe	United King dom	Enteritidis	2066	1.2.3.38.38.38.413	✓	✓	✓
SAL_BA9293AA	21783	SRR1969436	2014	6	5	Europe	United King dom	Enteritidis	30553	1.2.3.38.38.38.38	✓	✓	✓
SAL_BA9114AA	21779	SRR1969526	2014	6	12	Europe	United King dom	Enteritidis	6743	1.2.3.38.38.38.38	✓	✓	✓
SAL_BA8951AA	36530	SRR1969546	2014	7	28	Europe	United King dom	Enteritidis	2066	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA8852AA	32460	SRR1969597	2014	7	16	Europe	United King dom	Enteritidis	30907	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA8844AA	31652	SRR1969601	2014	7	9	Europe	United King dom	Enteritidis	30913	1.2.3.38.38.38.393	✓	✓	✓
SAL_BA8588AA	37799	SRR1969732	2014	8	1	Europe	United King dom	Enteritidis	31113	1.2.3.38.38.38.367	✓	✓	✓

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SAL_BA8536AA	36516	SRR1969758	2014	7	21	Europe	United Kingdom	Enteritidis	2747	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA8449AA	37829	SRR1969802	2014	7	28	Europe	United Kingdom	Enteritidis	28289	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA8444AA	37815	SRR1969805	2014	7	30	Europe	United Kingdom	Enteritidis	28289	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA8378AA	37826	SRR1969838	2014	7	28	Europe	United Kingdom	Enteritidis	2066	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA8205AA	34204	SRR1969924	2014	7	28	Europe	United Kingdom	Enteritidis	31423	1.2.3.38.38.38.1595	✓	✓	✓
SAL_BA8150AA	32467	SRR1969951	2014	7	19	Europe	United Kingdom	Enteritidis	31456	1.2.3.38.38.38.703	✓	✓	✓
SAL_BA7885AA	38410	SRR1970082	2014	8	1	Europe	United Kingdom	Enteritidis	31578	1.2.3.38.38.38.483	✓	✓	✓
SAL_BA7786AA	38349	SRR1970133	2014	7	27	Europe	United Kingdom	Enteritidis	31658	1.2.3.38.38.38.1378	✓	✓	✓
SAL_BA7695AA	34182	SRR1970179	2014	7	24	Europe	United Kingdom	Enteritidis	31704	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA7689AA	37830	SRR1970182	2014	7	30	Europe	United Kingdom	Enteritidis	31707	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA7611AA	31927	SRR1970220	2014	7	22	Europe	United Kingdom	Enteritidis	2066	1.2.3.38.38.38.367	✓	✓	✓

SAL_BA7600AA	46584	SRR1970226	2014	7	17	Europe	United Kingdom	Enteritidis	3175	1.2.3.38.38.38.393	✓	✓	✓
SAL_BA7479AA	29391	SRR1970288	2014	7	14	Europe	United Kingdom	Enteritidis	3181	1.2.3.38.38.38.393	✓	✓	✓
SAL_BA7469AA	37824	SRR1970294	2014	7	27	Europe	United Kingdom	Enteritidis	2066	1.2.3.38.38.38.367	✓	✓	✓
SAL_BA7461AA	38345	SRR1970302	2014	7	28	Europe	United Kingdom	Enteritidis	7153	1.2.3.38.38.38.393	✓	✓	✓
SAL_BA7442AA	46581	SRR1970321	2014	7	18	Europe	United Kingdom	Enteritidis	3184	1.2.3.38.38.38.367	✓	✓	✓
SAL_EA8049AA	18557	SRR3048580	2014	6	6	Europe	United Kingdom	Enteritidis	6818	1.2.3.38.38.38.38	✓	✓	✓
SAL_EA8008AA	56935	SRR3048716	2014	8	1	Europe	United Kingdom	Enteritidis	2066	1.2.3.38.38.38.413	✓	✓	✓
SAL_EA7962AA	21810	SRR3048785	2014	6	6	Europe	United Kingdom	Enteritidis	6902	1.2.3.38.38.38.38	✓	✓	✓
SAL_EA7824AA	29970	SRR3048933	2014	7	21	Europe	United Kingdom	Enteritidis	7033	1.2.3.38.38.38.367	✓	✓	✓
SAL_EA7699AA	29280	SRR3049070	2014	7	11	Europe	United Kingdom	Enteritidis	7153	1.2.3.38.38.38.393	✓	✓	✓
SAL_EA7675AA	21117	SRR3049094	2014	6	4	Europe	United Kingdom	Enteritidis	7177	1.2.3.38.38.38.38	✓	✓	✓
SAL_EA7665AA	20909	SRR3049104	2014	4	6	Europe	United Kingdom	Enteritidis	6744	1.2.3.38.38.38.38	✓	✓	✓
SAL_EA7540AA	21868	SRR3049229	2014	6	11	Europe	United Kingdom	Enteritidis	7309	1.2.3.38.38.38.2660	✓	✓	✓

SAL_EA7504AA	18555	SRR3049265	2014	6	6	Europe	United Kingdom	Enteritidis	734	1.2.3.38.38.38.38	✓	✓	✓
SAL_EA7467AA	21116	SRR3049304	2014	6	4	Europe	United Kingdom	Enteritidis	738	1.2.3.38.38.38.1775	✓	✓	✓
SAL_EA7408AA	18554	SRR3049366	2014	6	6	Europe	United Kingdom	Enteritidis	745	1.2.3.38.38.38.38	✓	✓	✓
SAL_EA7367AA	29281	SRR3049409	2014	7	11	Europe	United Kingdom	Enteritidis	747	1.2.3.38.38.38.393	✓	✓	✓
SAL_EA7334AA	20925	SRR3049443	2014	6	6	Europe	United Kingdom	Enteritidis	674	1.2.3.38.38.38.38	✓	✓	✓
SAL_EA7277AA	20926	SRR3049503	2014	6	7	Europe	United Kingdom	Enteritidis	755	1.2.3.38.38.38.2103	✓	✓	✓
SAL_EA7237AA	20927	SRR3049543	2014	6	8	Europe	United Kingdom	Enteritidis	759	1.2.3.38.38.38.38	✓	✓	✓
SAL_EA7167AA	34190	SRR3049621	2014	7	24	Europe	United Kingdom	Enteritidis	766	1.2.3.38.38.38.367	✓	✓	✓
SAL_EA7135AA	21843	SRR3049661	2014	6	1	Europe	United Kingdom	Enteritidis	674	1.2.3.38.38.38.38	✓	✓	✓
SAL_EA7086AA	29972	SRR3049720	2014	7	21	Europe	United Kingdom	Enteritidis	773	1.2.3.38.38.38.367	✓	✓	✓
SAL_EA7083AA	21844	SRR3049723	2014	6	10	Europe	United Kingdom	Enteritidis	773	1.2.3.38.38.38.38	✓	✓	✓
SAL_EA6989AA	21114	SRR3049844	2014	6	4	Europe	United Kingdom	Enteritidis	782	1.2.3.38.38.38.38	✓	✓	✓
SAL_EA6943AA	21113	SRR3049901	2014	6	4	Europe	United Kingdom	Enteritidis	787	1.2.3.38.38.38.1449	✓	✓	✓
SAL_EA6911AA	21815	SRR3049937	2014	6	9	Europe	United Kingdom	Enteritidis	790	1.2.3.38.38.38.38	✓	✓	✓

SAL_EA6910AA	21115	SRR3049939	2014	6	4	Europe	United Kingdom	Enteritidis	7902	1.2.3.38.38.38.38	✓	✓	✓
SAL_EA9314AA	38368	SRR3120716	2014	7	31	Europe	United Kingdom	Enteritidis	5791	1.2.3.38.38.38.367	✓	✓	✓
SAL_CA2175AA	21767	SRR1967796	2014	6	4	Europe	United Kingdom	Enteritidis	28504	1.2.3.38.38.38.38	✓		✓
SAL_CA4703AA	31926	SRR1965207	2014	7		Europe	United Kingdom	Enteritidis	26303				✓
SAL_CA2567AA	36499	SRR1967404	2014	7		Europe	United Kingdom	Enteritidis	28167				✓
SAL_CA2505AA	38312	SRR1967466	2014	8		Europe	United Kingdom	Enteritidis	28218				✓
SAL_CA0560AA	31924	SRR1968701	2014	7		Europe	United Kingdom	Enteritidis	29540				✓
SAL_CA0240AA	31930	SRR1968863	2014	7		Europe	United Kingdom	Enteritidis	29815				✓
SAL_BA7675AA	57104	SRR1970189	2014	8		Europe	United Kingdom	Enteritidis	31713				✓
SAL_EA7611AA	21813	SRR3049158				Europe	United Kingdom	Enteritidis	72338				✓
SAL_EA9317AA	36461	SRR3120711				Europe	United Kingdom	Enteritidis	57889				✓
SAL_CA6794AA	44683	SRR1957774	2014	8	29	Europe	United Kingdom	Enteritidis	24493	1.2.3.38.38.38.1469	✓	✓	

SAL_CA6754AA	45262	SRR1957814	2014	9	1	Europe	United Kingdom	Enteritidis	24533	1.2.3.38.38.38.461	✓	✓
SAL_CA6748AA	49751	SRR1957820	2014	9	15	Europe	United Kingdom	Enteritidis	24538	1.2.3.38.38.38.2163	✓	✓
SAL_CA6726AA	62582	SRR1957842	2014	9	2	Europe	United Kingdom	Enteritidis	24558	1.2.3.38.38.38.1404	✓	✓
SAL_CA6716AA	62574	SRR1957852	2014	9	1	Europe	United Kingdom	Enteritidis	24568	1.2.3.38.38.38.461	✓	✓
SAL_CA6691AA	62581	SRR1957877	2014	8	27	Europe	United Kingdom	Enteritidis	24591	1.2.3.38.38.38.550	✓	✓
SAL_CA6680AA	48262	SRR1957888	2014	9	5	Europe	United Kingdom	Enteritidis	24601	1.2.3.38.38.38.367	✓	✓
SAL_CA6582AA	46118	SRR1957986	2014	8	20	Europe	United Kingdom	Enteritidis	24693	1.2.3.38.38.38.550	✓	✓
SAL_CA6557AA	58510	SRR1958011	2014	10	2	Europe	United Kingdom	Enteritidis	73167	1.2.3.38.38.38.655	✓	✓
SAL_CA6541AA	46085	SRR1958028	2014	8	19	Europe	United Kingdom	Enteritidis	24732	1.2.3.38.38.38.550	✓	✓
SAL_CA6536AA	50109	SRR1958033	2014	9	16	Europe	United Kingdom	Enteritidis	24738	1.2.3.38.38.38.787	✓	✓
SAL_CA6517AA	57623	SRR1958052	2014	8	8	Europe	United Kingdom	Enteritidis	20066	1.2.3.38.38.38.367	✓	✓
SAL_CA6439AA	48206	SRR1958131	2014	9	4	Europe	United Kingdom	Enteritidis	24848	1.2.3.38.38.38.550	✓	✓

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SAL_CA6369AA	50158	SRR1958208	2014	9	20	Europe	United Kingdom	Enteritidis	2066	1.2.3.38.38.38.413	✓	✓
SAL_CA6358AA	57641	SRR1958219	2014	9	26	Europe	United Kingdom	Enteritidis	7317	1.2.3.38.38.38.655	✓	✓
SAL_CA6305AA	62610	SRR1958272	2014	10	30	Europe	United Kingdom	Enteritidis	24946	1.2.3.38.38.38.653	✓	✓
SAL_CA6297AA	66845	SRR1958280	2014	10	13	Europe	United Kingdom	Enteritidis	7317	1.2.3.38.38.38.544	✓	✓
SAL_CA6117AA	62554	SRR1958460	2014	8	24	Europe	United Kingdom	Enteritidis	25112	1.2.3.38.38.38.550	✓	✓
SAL_CA6073AA	60382	SRR1958504	2014	10	7	Europe	United Kingdom	Enteritidis	7317	1.2.3.38.38.38.2034	✓	✓
SAL_CA6031AA	46156	SRR1958546	2014	8	19	Europe	United Kingdom	Enteritidis	25187	1.2.3.38.38.38.550	✓	✓
SAL_CA5963AA	62556	SRR1958614	2014	8	29	Europe	United Kingdom	Enteritidis	25250	1.2.3.38.38.38.1151	✓	✓
SAL_CA5901AA	60074	SRR1958676	2014	10	9	Europe	United Kingdom	Enteritidis	7317	1.2.3.38.38.38.655	✓	✓
SAL_CA5598AA	69743	SRR1960032	2014	11	13	Europe	United Kingdom	Enteritidis	25562	1.2.3.38.38.38.484	✓	✓
SAL_CA5222AA	74309	SRR1963071	2014	11	27	Europe	United Kingdom	Enteritidis	7317	1.2.3.38.38.38.458	✓	✓
SAL_CA5115AA	69699	SRR1963272	2014	11	12	Europe	United Kingdom	Enteritidis	24946	1.2.3.38.38.38.653	✓	✓

SAL_CA4837AA	34180	SRR1965068	2014	7	17	Europe	United Kingdom	Enteritidis	26182	1.2.3.38.38.38.624	✓	✓
SAL_CA4792AA	57102	SRR1965114	2014	8	11	Europe	United Kingdom	Enteritidis	26222	1.2.3.38.38.38.367	✓	✓
SAL_CA4785AA	32476	SRR1965122	2014	7	17	Europe	United Kingdom	Enteritidis	26229	1.2.3.38.38.38.393	✓	✓
SAL_CA4697AA	50356	SRR1965213	2014	9	5	Europe	United Kingdom	Enteritidis	26308	1.2.3.38.38.38.624	✓	✓
SAL_CA4642AA	53110	SRR1965275	2014	9	23	Europe	United Kingdom	Enteritidis	26355	1.2.3.38.38.38.354	✓	✓
SAL_CA4605AA	21785	SRR1965313	2014	6	3	Europe	United Kingdom	Enteritidis	26390	1.2.3.38.38.38.38	✓	✓
SAL_CA4591AA	52954	SRR1965327	2014	9	25	Europe	United Kingdom	Enteritidis	26402	1.2.3.38.38.38.655	✓	✓
SAL_CA4580AA	37759	SRR1965339	2014	7	28	Europe	United Kingdom	Enteritidis	5144	1.2.3.38.38.38.570	✓	✓
SAL_CA4509AA	65448	SRR1965411	2014	10	3	Europe	United Kingdom	Enteritidis	26469	1.2.3.38.38.38.2246	✓	✓
SAL_CA4476AA	40327	SRR1965444	2014	8	18	Europe	United Kingdom	Enteritidis	26498	1.2.3.38.38.38.550	✓	✓
SAL_CA4438AA	24053	SRR1965483	2014	6	19	Europe	United Kingdom	Enteritidis	26531	1.2.3.38.38.38.1166	✓	✓
SAL_CA4437AA	43431	SRR1965484	2014	8	29	Europe	United	Enteritidis	2665	1.2.3.38.38.38.458	✓	✓

							King dom		32			
SAL_CA4427AA	38309	SRR1965496	2014	7	28	Europe	United King dom	Enterit idis	2654 2	1.2.3.38.38.38.413	✓	✓
SAL_CA4394AA	37778	SRR1965530	2014	8	1	Europe	United King dom	Enterit idis	7612	1.2.3.38.38.38.367	✓	✓
SAL_CA4361AA	31977	SRR1965563	2014	4	22	Europe	United King dom	Enterit idis	514	1.2.3.38.38.38.790	✓	✓
SAL_CA4317AA	36473	SRR1965618	2014	7	21	Europe	United King dom	Enterit idis	2663 4	1.2.3.38.38.38.746	✓	✓
SAL_CA4268AA	36506	SRR1965669	2014	7	24	Europe	United King dom	Enterit idis	2667 8	1.2.3.38.38.38.461	✓	✓
SAL_CA4213AA	37062	SRR1965730	2014	8	6	Europe	United King dom	Enterit idis	2672 3	1.2.3.38.38.38.1201	✓	✓
SAL_CA4209AA	65449	SRR1965735	2014	8	1	Europe	United King dom	Enterit idis	2672 7	1.2.3.38.38.38.413	✓	✓
SAL_CA4203AA	40269	SRR1965742	2014	8	9	Europe	United King dom	Enterit idis	2673 3	1.2.3.38.38.38.1162	✓	✓
SAL_CA4194AA	46009	SRR1965753	2014	8	9	Europe	United King dom	Enterit idis	2511 2	1.2.3.38.38.38.550	✓	✓
SAL_CA4174AA	65379	SRR1965774	2014	9	29	Europe	United King dom	Enterit idis	2675 9	1.2.3.38.38.38.728	✓	✓
SAL_CA4165AA	57112	SRR1965784	2014	8	1	Europe	United King dom	Enterit idis	2676 8	1.2.3.38.38.38.413	✓	✓

SAL_CA4088AA	31952	SRR1965867	2014	7	24	Europe	United Kingdom	Enteritidis	512	1.2.3.38.38.38.550	✓	✓
SAL_CA4077AA	91893	SRR1965879	2014	8	1	Europe	United Kingdom	Enteritidis	2684	1.2.3.38.38.38.413	✓	✓
SAL_CA4061AA	31969	SRR1965895	2014	7	25	Europe	United Kingdom	Enteritidis	2685	1.2.3.38.38.38.624	✓	✓
SAL_CA3956AA	23500	SRR1966002	2014	6	17	Europe	United Kingdom	Enteritidis	2695	1.2.3.38.38.38.949	✓	✓
SAL_CA3943AA	39486	SRR1966020	2014	8	4	Europe	United Kingdom	Enteritidis	2696	1.2.3.38.38.38.1184	✓	✓
SAL_CA3934AA	26644	SRR1966029	2014	6	30	Europe	United Kingdom	Enteritidis	2697	1.2.3.38.38.38.472	✓	✓
SAL_CA3888AA	37835	SRR1966076	2014	7	28	Europe	United Kingdom	Enteritidis	2701	1.2.3.38.38.38.1127	✓	✓
SAL_CA3887AA	36504	SRR1966077	2014	7	23	Europe	United Kingdom	Enteritidis	2701	1.2.3.38.38.38.544	✓	✓
SAL_CA3862AA	25260	SRR1966102	2014	7	7	Europe	United Kingdom	Enteritidis	2703	1.2.3.38.38.38.550	✓	✓
SAL_CA3715AA	34187	SRR1966252	2014	7	25	Europe	United Kingdom	Enteritidis	2716	1.2.3.38.38.38.367	✓	✓
SAL_CA3678AA	32477	SRR1966289	2014	7	17	Europe	United Kingdom	Enteritidis	2719	1.2.3.38.38.38.393	✓	✓
SAL_CA3660AA	40794	SRR1966307	2014	8	12	Europe	United	Enteritidis	272	1.2.3.38.38.38.478	✓	✓

							King dom		14			
SAL_CA3622AA	57113	SRR1966345	2014	8	5	Europe	United King dom	Enterit idis	2724	1.2.3.38.38.38.413	✓	✓
SAL_CA3616AA	5355	SRR1966351	2014	4	2	Europe	United King dom	Enterit idis	7317	1.3.154.272.272.272.272	✓	✓
SAL_CA3519AA	39449	SRR1966447	2014	7	21	Europe	United King dom	Enterit idis	2734	1.2.3.38.38.38.367	✓	✓
SAL_CA3484AA	21781	SRR1966482	2014	6	2	Europe	United King dom	Enterit idis	2737	1.2.3.38.38.38.729	✓	✓
SAL_CA3475AA	37822	SRR1966491	2014	7	30	Europe	United King dom	Enterit idis	2738	1.2.3.38.38.38.393	✓	✓
SAL_CA3464AA	36392	SRR1966502	2014	8	4	Europe	United King dom	Enterit idis	2739	1.2.3.38.38.38.488	✓	✓
SAL_CA3431AA	68972	SRR1966536	2014	11	11	Europe	United King dom	Enterit idis	7317	1.2.3.38.38.38.2646	✓	✓
SAL_CA3345AA	56112	SRR1966625	2014	9	12	Europe	United King dom	Enterit idis	2749	1.2.3.38.38.38.354	✓	✓
SAL_CA3342AA	73134	SRR1966628	2014	12	1	Europe	United King dom	Enterit idis	2749	1.2.3.38.38.38.2129	✓	✓
SAL_CA3286AA	32470	SRR1966685	2014	7	17	Europe	United King dom	Enterit idis	2754	1.2.3.38.38.38.367	✓	✓
SAL_CA3256AA	38772	SRR1966715	2014	8	6	Europe	United King dom	Enterit idis	2757	1.2.3.38.38.38.413	✓	✓

SAL_CA3226AA	37111	SRR1966745	2014	8	6	Europe	United Kingdom	Enteritidis	27599	1.2.3.38.38.38.1431	✓	✓
SAL_CA3113AA	21786	SRR1966858	2014	6	3	Europe	United Kingdom	Enteritidis	6744	1.2.3.38.38.38.38	✓	✓
SAL_CA3060AA	73221	SRR1966911	2014	12	8	Europe	United Kingdom	Enteritidis	27738	1.2.3.38.38.38.970	✓	✓
SAL_CA3043AA	34171	SRR1966928	2014	7	24	Europe	United Kingdom	Enteritidis	27755	1.2.3.38.38.38.2245	✓	✓
SAL_CA3036AA	14128	SRR1966935	2014	5	22	Europe	United Kingdom	Enteritidis	27761	1.2.3.38.38.38.949	✓	✓
SAL_CA2987AA	27067	SRR1966984	2014	7	7	Europe	United Kingdom	Enteritidis	6744	1.2.3.38.38.38.38	✓	✓
SAL_CA2933AA	37814	SRR1967038	2014	7	30	Europe	United Kingdom	Enteritidis	27851	1.2.3.38.38.38.367	✓	✓
SAL_CA2925AA	46582	SRR1967046	2014	7	16	Europe	United Kingdom	Enteritidis	27858	1.2.3.38.38.38.393	✓	✓
SAL_CA2918AA	34198	SRR1967053	2014	7	24	Europe	United Kingdom	Enteritidis	27863	1.2.3.38.38.38.1153	✓	✓
SAL_CA2895AA	52972	SRR1967076	2014	9	26	Europe	United Kingdom	Enteritidis	20666	1.2.3.38.38.38.413	✓	✓
SAL_CA2850AA	65390	SRR1967121	2014	9	12	Europe	United Kingdom	Enteritidis	24946	1.2.3.38.38.38.653	✓	✓
SAL_CA2840AA	31611	SRR1967131	2014	7	14	Europe	United Kingdom	Enteritidis	27925	1.2.3.38.38.38.394	✓	✓

SAL_CA2802AA	61859	SRR1967169	2014	10	10	Europe	United Kingdom	Enteritidis	279581	1.2.3.38.38.38.571	✓	✓
SAL_CA2784AA	34202	SRR1967187	2014	7	21	Europe	United Kingdom	Enteritidis	279751	1.2.3.38.38.38.393	✓	✓
SAL_CA2755AA	32525	SRR1967216	2014	7	18	Europe	United Kingdom	Enteritidis	280000	1.2.3.38.38.38.367	✓	✓
SAL_CA2710AA	38411	SRR1967261	2014	7	30	Europe	United Kingdom	Enteritidis	280037	1.2.3.38.38.38.544	✓	✓
SAL_CA2687AA	39515	SRR1967284	2014	8	11	Europe	United Kingdom	Enteritidis	280056	1.2.3.38.38.38.550	✓	✓
SAL_CA2650AA	40324	SRR1967321	2014	8	18	Europe	United Kingdom	Enteritidis	280090	1.2.3.38.38.38.550	✓	✓
SAL_CA2577AA	57103	SRR1967394	2014	7	31	Europe	United Kingdom	Enteritidis	281573	1.2.3.38.38.38.413	✓	✓
SAL_CA2549AA	14099	SRR1967422	2014	5	21	Europe	United Kingdom	Enteritidis	281882	1.2.3.38.38.38.949	✓	✓
SAL_CA2493AA	36476	SRR1967478	2014	7	21	Europe	United Kingdom	Enteritidis	761212	1.2.3.38.38.38.746	✓	✓
SAL_CA2461AA	38718	SRR1967510	2014	8	7	Europe	United Kingdom	Enteritidis	282254	1.2.3.38.38.38.1288	✓	✓
SAL_CA2438AA	32375	SRR1967533	2014	7	18	Europe	United Kingdom	Enteritidis	715353	1.2.3.38.38.38.393	✓	✓
SAL_CA2431AA	24987	SRR1967540	2014	6	28	Europe	United Kingdom	Enteritidis	282	1.2.3.38.38.38.472	✓	✓

									83		
SAL_CA2374AA	57130	SRR1967597	2014	9	30	Europe	United Kingdom	Enteritidis	2833 2	1.2.3.38.38.38.653	✓ ✓
SAL_CA2346AA	36385	SRR1967625	2014	8	4	Europe	United Kingdom	Enteritidis	7317	1.2.3.38.38.38.544	✓ ✓
SAL_CA2242AA	32464	SRR1967729	2014	7	17	Europe	United Kingdom	Enteritidis	2844 5	1.2.3.38.38.38.544	✓ ✓
SAL_CA2170AA	50360	SRR1967801	2014	9	3	Europe	United Kingdom	Enteritidis	2850 9	1.2.3.38.38.38.653	✓ ✓
SAL_CA1887AA	39447	SRR1967990	2014	7	18	Europe	United Kingdom	Enteritidis	2867 6	1.2.3.38.38.38.570	✓ ✓
SAL_CA1882AA	36394	SRR1967993	2014	8	4	Europe	United Kingdom	Enteritidis	2066	1.2.3.38.38.38.367	✓ ✓
SAL_CA1871AA	37006	SRR1967999	2014	8	3	Europe	United Kingdom	Enteritidis	2868 4	1.2.3.38.38.38.653	✓ ✓
SAL_CA1747AA	42171	SRR1968063	2014	8	26	Europe	United Kingdom	Enteritidis	2873 9	1.2.3.38.38.38.1544	✓ ✓
SAL_CA1735AA	65373	SRR1968069	2014	10	2	Europe	United Kingdom	Enteritidis	2874 4	1.2.3.38.38.38.790	✓ ✓
SAL_CA1318AA	25320	SRR1968299	2014	6	24	Europe	United Kingdom	Enteritidis	2905 0	1.2.3.38.38.38.472	✓ ✓
SAL_CA1311AA	9310	SRR1968303	2014	4	23	Europe	United Kingdom	Enteritidis	2905 4	1.3.6.6.6.6.6	✓ ✓

SAL_CA1299AA	40273	SRR1968309	2014	8	12	Europe	United Kingdom	Enteritidis	290604	1.2.3.38.38.38.1151	✓	✓
SAL_CA1278AA	57111	SRR1968319	2014	8	1	Europe	United Kingdom	Enteritidis	290704	1.2.3.38.38.38.1365	✓	✓
SAL_CA1258AA	31965	SRR1968329	2014	7	25	Europe	United Kingdom	Enteritidis	200666	1.2.3.38.38.38.367	✓	✓
SAL_CA1168AA	13389	SRR1968417	2014	5	12	Europe	United Kingdom	Enteritidis	291584	1.2.3.38.38.38.962	✓	✓
SAL_CA1162AA	34203	SRR1968423	2014	7	21	Europe	United Kingdom	Enteritidis	291664	1.2.3.38.38.38.393	✓	✓
SAL_CA1093AA	31975	SRR1968475	2014	7	25	Europe	United Kingdom	Enteritidis	292112	1.2.3.38.38.38.1903	✓	✓
SAL_CA0903AA	40224	SRR1968520	2014	8	13	Europe	United Kingdom	Enteritidis	292555	1.2.3.38.38.38.413	✓	✓
SAL_CA0844AA	36364	SRR1968553	2014	7	30	Europe	United Kingdom	Enteritidis	51414	1.2.3.38.38.38.910	✓	✓
SAL_CA0741AA	65434	SRR1968603	2014	9	30	Europe	United Kingdom	Enteritidis	731417	1.2.3.38.38.38.655	✓	✓
SAL_CA0720AA	40274	SRR1968614	2014	8	11	Europe	United Kingdom	Enteritidis	294066	1.2.3.38.38.38.766	✓	✓
SAL_CA0650AA	25266	SRR1968651	2014	7	1	Europe	United Kingdom	Enteritidis	51412	1.2.3.38.38.38.550	✓	✓
SAL_CA0634AA	36475	SRR1968659	2014	7	21	Europe	United Kingdom	Enteritidis	294882	1.2.3.38.38.38.746	✓	✓

SAL_CA0607AA	31656	SRR1968675	2014	7	10	Europe	United Kingdom	Enteritidis	29502	1.2.3.38.38.38.533	✓ ✓
SAL_CA0461AA	46011	SRR1968755	2014	8	9	Europe	United Kingdom	Enteritidis	20666	1.2.3.38.38.38.367	✓ ✓
SAL_CA0414AA	36477	SRR1968778	2014	7	21	Europe	United Kingdom	Enteritidis	20666	1.2.3.38.38.38.367	✓ ✓
SAL_CA0401AA	37037	SRR1968785	2014	8		Europe	France	Enteritidis	29673	1.2.3.38.38.38.1098	✓ ✓
SAL_CA0389AA	23057	SRR1968791	2014	6	7	Europe	United Kingdom	Enteritidis	29684	1.2.3.38.38.38.413	✓ ✓
SAL_CA0358AA	21782	SRR1968806	2014	6	2	Europe	United Kingdom	Enteritidis	29714	1.2.3.38.38.38.38	✓ ✓
SAL_CA0356AA	13835	SRR1968807	2014	5	15	Europe	United Kingdom	Enteritidis	29715	1.1.2.1074.1763.2074.3174	✓ ✓
SAL_CA0161AA	37800	SRR1968900	2014	7	29	Europe	United Kingdom	Enteritidis	29862	1.2.3.38.38.38.367	✓ ✓
SAL_CA0138AA	40795	SRR1968912	2014	8	15	Europe	United Kingdom	Enteritidis	25250	1.2.3.38.38.38.766	✓ ✓
SAL_CA0102AA	37036	SRR1968931	2014	8		Europe	France	Enteritidis	55151	1.2.3.38.38.38.600	✓ ✓
SAL_CA0022AA	31623	SRR1968972	2014	7	9	Europe	United Kingdom	Enteritidis	29978	1.2.3.38.38.38.38	✓ ✓
SAL_BA9958AA	27797	SRR1969004	2014	6	27	Europe	United Kingdom	Enteritidis	30026	1.2.3.38.38.38.38	✓ ✓

SAL_BA9836AA	57110	SRR1969068	2014	8	1	Europe	United Kingdom	Enteritidis	301241	1.2.3.38.38.38.413	✓	✓
SAL_BA9661AA	32478	SRR1969172	2014	7	17	Europe	United Kingdom	Enteritidis	302553	1.2.3.38.38.38.393	✓	✓
SAL_BA9625AA	39514	SRR1969190	2014	8	14	Europe	United Kingdom	Enteritidis	302880	1.2.3.38.38.38.413	✓	✓
SAL_BA9621AA	65125	SRR1969192	2014	11	4	Europe	United Kingdom	Enteritidis	302884	1.2.3.38.38.38.653	✓	✓
SAL_BA9589AA	43427	SRR1969209	2014	8	28	Europe	United Kingdom	Enteritidis	303111	1.2.3.38.38.38.461	✓	✓
SAL_BA9550AA	32550	SRR1969229	2014	7	18	Europe	United Kingdom	Enteritidis	303444	1.2.3.38.38.38.393	✓	✓
SAL_BA9457AA	41995	SRR1969283	2014	8	20	Europe	United Kingdom	Enteritidis	304117	1.2.3.38.38.38.413	✓	✓
SAL_BA9372AA	46593	SRR1969365	2014	7	15	Europe	United Kingdom	Enteritidis	304889	1.2.3.38.38.38.1608	✓	✓
SAL_BA9351AA	37038	SRR1969386	2014	8		Europe	France	Enteritidis	305062	1.2.3.38.38.38.2314	✓	✓
SAL_BA9138AA	39506	SRR1969515	2014	8	8	Europe	United Kingdom	Enteritidis	306893	1.2.3.38.38.38.367	✓	✓
SAL_BA9133AA	23082	SRR1969517	2014	6	8	Europe	United Kingdom	Enteritidis	306944	1.2.3.38.38.38.1315	✓	✓

SAL_BA8887AA	38428	SRR1969578	2014	7	29	Europe	United Kingdom	Enteritidis	308791	1.2.3.38.38.38.550	✓	✓
SAL_BA8669AA	36528	SRR1969692	2014	7	28	Europe	United Kingdom	Enteritidis	310571	1.2.3.38.38.38.436	✓	✓
SAL_BA8636AA	32475	SRR1969708	2014	7	17	Europe	United Kingdom	Enteritidis	310888	1.2.3.38.38.38.2060	✓	✓
SAL_BA8627AA	37035	SRR1969713	2014	8		Europe	France	Enteritidis	310961	1.2.3.38.38.38.673	✓	✓
SAL_BA8576AA	31612	SRR1969738	2014	7	14	Europe	United Kingdom	Enteritidis	311141	1.2.3.38.38.38.394	✓	✓
SAL_BA8545AA	31613	SRR1969753	2014	7	14	Europe	United Kingdom	Enteritidis	311165	1.2.3.38.38.38.38	✓	✓
SAL_BA8376AA	36474	SRR1969839	2014	7	21	Europe	United Kingdom	Enteritidis	206661	1.2.3.38.38.38.367	✓	✓
SAL_BA8364AA	37007	SRR1969845	2014	8	1	Europe	United Kingdom	Enteritidis	312988	1.2.3.38.38.38.393	✓	✓
SAL_BA8273AA	38430	SRR1969891	2014	8	1	Europe	Jersey	Enteritidis	313661	1.2.3.38.38.38.367	✓	✓
SAL_BA8265AA	25225	SRR1969895	2014	7	28	Europe	United Kingdom	Enteritidis	313741	1.2.3.38.38.38.472	✓	✓
SAL_BA8197AA	41991	SRR1969928	2014	8	19	Europe	United Kingdom	Enteritidis	314431	1.2.3.38.38.38.550	✓	✓
SAL_BA8189AA	23507	SRR1969932	2014	6	19	Europe	United	Enteritidis	31414	1.2.3.38.38.38.962	✓	✓

							King dom		39			
SAL_BA8017AA	38773	SRR1970014	2014	8	7	Europe	United King dom	Enterit idis	3151	1.2.3.38.38.38.413	✓	✓
SAL_BA7794AA	37806	SRR1970129	2014	7	30	Europe	United King dom	Enterit idis	3165	1.2.3.38.38.38.1162	✓	✓
SAL_BA7770AA	39446	SRR1970141	2014	7	12	Europe	United King dom	Enterit idis	3166	1.2.3.38.38.38.393	✓	✓
SAL_BA7725AA	31981	SRR1970163	2014	7	25	Europe	United King dom	Enterit idis	2066	1.2.3.38.38.38.367	✓	✓
SAL_EA8050AA	21845	SRR3048579	2014	6	10	Europe	United King dom	Enterit idis	6817	1.2.3.38.38.38.38	✓	✓
SAL_EA7904AA	43909	SRR3048844	2014	8	21	Europe	United King dom	Enterit idis	6957	1.2.3.38.38.38.413	✓	✓
SAL_EA7808AA	46125	SRR3048951	2014	8	23	Europe	United King dom	Enterit idis	7049	1.2.3.38.38.38.550	✓	✓
SAL_EA7763AA	21132	SRR3048999	2014	5	31	Europe	United King dom	Enterit idis	7091	1.2.3.38.38.38.2669	✓	✓
SAL_EA7752AA	58576	SRR3049014	2014	9	28	Europe	United King dom	Enterit idis	7102	1.2.3.38.38.38.1418	✓	✓
SAL_EA7702AA	53036	SRR3049067	2014	9	23	Europe	United King dom	Enterit idis	6744	1.2.3.38.38.38.38	✓	✓
SAL_EA7701AA	56991	SRR3049068	2014	9	30	Europe	United King dom	Enterit idis	7151	1.2.3.38.38.38.2244	✓	✓
SAL_EA7677AA	21119	SRR3049092	2014	6	4	Europe	United King dom	Enterit idis	7175	1.2.3.38.38.38.2483	✓	✓
SAL_EA7644AA	43884	SRR3049125	2014	8	13	Europe	United King dom	Enterit idis	7205	1.2.3.38.38.38.2366	✓	✓

SAL_EA7635AA	43930	SRR3049134	2014	8	14	Europe	United Kingdom	Enteritidis	721	1.2.3.38.38.38.1795	✓	✓
SAL_EA7599AA	48161	SRR3049170	2014	8	24	Europe	United Kingdom	Enteritidis	725	1.2.3.38.38.38.550	✓	✓
SAL_EA7582AA	43936	SRR3049187	2014	8	21	Europe	United Kingdom	Enteritidis	726	1.2.3.38.38.38.1151	✓	✓
SAL_EA7578AA	21846	SRR3049191	2014	6	9	Europe	United Kingdom	Enteritidis	727	1.2.3.38.38.38.38	✓	✓
SAL_EA7449AA	46155	SRR3049322	2014	8	27	Europe	United Kingdom	Enteritidis	739	1.2.3.38.38.38.461	✓	✓
SAL_EA7409AA	45269	SRR3049365	2014	8	27	Europe	United Kingdom	Enteritidis	743	1.2.3.38.38.38.550	✓	✓
SAL_EA7284AA	43925	SRR3049494	2014	8	13	Europe	United Kingdom	Enteritidis	754	1.2.3.38.38.38.1351	✓	✓
SAL_EA7278AA	20929	SRR3049502	2014	6	3	Europe	United Kingdom	Enteritidis	755	1.2.3.38.38.38.550	✓	✓
SAL_EA7267AA	43958	SRR3049513	2014	8	18	Europe	United Kingdom	Enteritidis	756	1.2.3.38.38.38.550	✓	✓
SAL_EA7231AA	39517	SRR3049549	2014	8	12	Europe	United Kingdom	Enteritidis	759	1.2.3.38.38.38.550	✓	✓
SAL_EA7216AA	29971	SRR3049565	2014	7	21	Europe	United Kingdom	Enteritidis	761	1.2.3.38.38.38.367	✓	✓
SAL_EA7084AA	43960	SRR3049722	2014	8	18	Europe	United Kingdom	Enteritidis	773	1.2.3.38.38.38.550	✓	✓
SAL_EA7071AA	18556	SRR3049743	2014	6	6	Europe	United Kingdom	Enteritidis	775	1.2.3.38.38.38.38	✓	✓
SAL_EA7047AA	29308	SRR3049775	2014	7	15	Europe	United Kingdom	Enteritidis	777	1.2.3.38.38.38.413	✓	✓

SAL_EA7041AA	25004	SRR3049783	2014	7	3	Europe	United Kingdom	Enteritidis	77 79	1.2.3.38.38.38.550	✓	✓
SAL_EA7034AA	1514	SRR3049796	2014	3	25	Europe	United Kingdom	Enteritidis	77 86	1.27.153.27 1.271.271.271	✓	✓
SAL_EA7020AA	43937	SRR3049811	2014	8	21	Europe	United Kingdom	Enteritidis	77 99	1.2.3.38.38.38.550	✓	✓
SAL_EA6983AA	21120	SRR3049851	2014	6	2	Europe	United Kingdom	Enteritidis	78 33	1.2.3.38.38.38.949	✓	✓
SAL_EA6940AA	21871	SRR3049904	2014	6	12	Europe	United Kingdom	Enteritidis	78 73	1.2.3.38.38.38.807	✓	✓
SAL_EA9321AA	43927	SRR3120707	2014	8	17	Europe	United Kingdom	Enteritidis	57 88	1.2.3.38.38.38.515	✓	✓
SAL_FA4108AA	21807	SRR3323014	2014	6	8	Europe	United Kingdom	Enteritidis	67 74	1.2.3.38.38.38.38	✓	✓
SAL_FA5451AA	21809	SRR3401403	2014	6	8	Europe	United Kingdom	Enteritidis	67 74	1.2.3.38.38.38.38	✓	✓
SAL_FA5597AA	05224	SRR3410208	2014			Europe	Germany	Enteritidis	54 45	1.2.3.38.38.38.686	✓	✓
SAL_FA5596AA	05225	SRR3410209	2014			Europe	Germany	Enteritidis	54 46	1.2.3.38.38.38.687	✓	✓
SAL_FA5595AA	05226	SRR3410210	2014			Europe	Germany	Enteritidis	54 47	1.2.3.38.38.38.2115	✓	✓
SAL_FA5594AA	05227	SRR3410211	2014			Europe	Germany	Enteritidis	54 48	1.2.3.38.38.38.685	✓	✓
SAL_FA5593AA	05795	SRR3410212	2014			Europe	Germany	Enteritidis	54 49	1.2.3.38.38.38.2801	✓	✓
SAL_FA5592AA	05946	SRR3410213	2014			Europe	Germany	Enteritidis	55 00	1.2.3.38.38.38.2799	✓	✓
SAL_FA5591AA	06012	SRR3410214	2014			Europe	Germany	Enteritidis	55 01	1.2.3.38.38.38.2798	✓	✓
SAL_FA5590AA	06175	SRR3410215	2014			Europe	Germany	Enteritidis	55 01	1.2.3.38.38.38.2800	✓	✓

SAL_FA5589AA	06388	SRR3410216	2014			Europe	Germany	Enteritidis	55	1.2.3.38.38.38.2797	✓	✓
SAL_FA5634AA	37045	SRR3417493	2014			Europe	Austria	Enteritidis	51	1.2.3.38.38.38.1757	✓	✓
SAL_FA5633AA	37046	SRR3417494	2014			Europe	Austria	Enteritidis	51	1.2.3.38.38.38.357	✓	✓
SAL_FA5632AA	37047	SRR3417495	2014			Europe	Austria	Enteritidis	51	1.2.3.38.38.38.413	✓	✓
SAL_FA5631AA	45605	SRR3417496	2014			Europe	Luxembourg	Enteritidis	51	1.2.3.38.38.38.790	✓	✓
SAL_FA5630AA	49691	SRR3417497	2014			Europe	Austria	Enteritidis	51	1.2.3.38.38.38.1111	✓	✓
SAL_FA5629AA	49692	SRR3417498	2014			Europe	Austria	Enteritidis	51	1.2.3.38.38.38.357	✓	✓
SAL_FA5628AA	49693	SRR3417499	2014			Europe	Austria	Enteritidis	51	1.2.3.38.38.38.357	✓	✓
SAL_FA5627AA	50104	SRR3417500	2014			Europe	Austria	Enteritidis	51	1.2.3.38.38.38.790	✓	✓
SAL_FA5626AA	53973	SRR3417501	2014			Europe	Germany	Enteritidis	51	1.2.3.38.38.38.1394	✓	✓
SAL_FA5625AA	53996	SRR3417502	2014			Europe	Germany	Enteritidis	52	1.2.3.38.38.38.1255	✓	✓
SAL_FA5624AA	54008	SRR3417503	2014			Europe	Germany	Enteritidis	52	1.2.3.38.38.38.533	✓	✓
SAL_FA5623AA	54014	SRR3417504	2014			Europe	Germany	Enteritidis	52	1.2.3.38.38.38.1555	✓	✓
SAL_FA5622AA	54038	SRR3417505	2014			Europe	Germany	Enteritidis	52	1.2.3.38.38.38.1555	✓	✓
SAL_FA5621AA	54047	SRR3417506	2014			Europe	Germany	Enteritidis	52	1.2.3.38.38.38.1438	✓	✓
SAL_FA5620AA	54053	SRR3417507	2014			Europe	Germany	Enteritidis	52	1.2.3.38.38.38.1255	✓	✓
SAL_FA5619AA	54059	SRR3417508	2014			Europe	Germany	Enteritidis	52	1.2.3.38.38.38.2623	✓	✓
SAL_EA8419AA	201405757	traces-0foIqty	2014	7	2	Europe	France	Enteritidis	55		✓	✓
SAL_EA8417AA	201405861	traces-0hvfoaj	2014	7	18	Europe	France	Enteritidis	55		✓	✓

SAL_EA8112AA	201405760	traces-0JiMSsi	2014	7	23	Europe	France	Enteritidis	51 2		✓	✓
SAL_EA8113AA	201405756	traces-0qWOdHp	2014	7	21	Europe	France	Enteritidis	55 4		✓	✓
SAL_EA8416AA	201405122	traces-0wRGnlX	2014	7	19	Europe	France	Enteritidis	55 3		✓	✓
SAL_DA1790AA	H12468035 1	SRR1635097	2012	11	7	Europe	United Kingdom	Enteritidis	20 19 5	1.1.185.343.343.343.343	✓	
SAL_DA1773AA	H12394064 9	SRR1635114	2012	9	21	Europe	United Kingdom	Enteritidis	20 21 1	1.6.11.13.333.333.333	✓	
SAL_DA1151AA	H12144032 2	SRR1645334	2012	3	26	Europe	United Kingdom	Enteritidis	20 75 5	13.29.164.288.288.288.288	✓	
SAL_DA1070AA	H12374051 9	SRR1645445	2012	9	3	Europe	United Kingdom	Enteritidis	20 83 3	1.1.176.315.315.315.812	✓	
SAL_DA0883AA	H12358052 1	SRR1645782	2012	8	22	Europe	United Kingdom	Enteritidis	21 00 2	1.1.177.321.321.321.321	✓	
SAL_DA0881AA	H12348047 4	SRR1645784	2012	8	21	Europe	United Kingdom	Enteritidis	21 00 4	3.4.49.318.318.318.318	✓	
SAL_DA0796AA	H12254066 9	SRR1645877	2012	6	16	Europe	United Kingdom	Enteritidis	21 08 3	1.5.170.299.299.299.299	✓	
SAL_DA0775AA	H12228036 6	SRR1645898	2012	5	29	Europe	United Kingdom	Enteritidis	21 10 3	1.5.166.294.294.294.294	✓	
SAL_DA0563AA	H12242030 4	SRR1646133	2012	6	7	Europe	United Kingdom	Enteritidis	21 30 3	1.1.168.297.297.297.297	✓	
SAL_DA0480AA	H12054	SRR1646243	2012	2	1	Europe	United	Enteritidis	21 13	1.1.162.286.286.286.286	✓	

	0611						United Kingdom		78		
SAL_DA0447AA	H12398039 1	SRR1646278	2012	9	17	Europe	United Kingdom	Enteritidis	2140 7	1.11.181.335.335.335	✓
SAL_CA6836AA	44755	SRR1957732	2014	9	10	Europe	United Kingdom	Enteritidis	2445 7	10.20.81.133.133.133.1 33	✓
SAL_CA6759AA	44692	SRR1957809	2014	9	8	Europe	United Kingdom	Enteritidis	1567 3	1.5.79.129.129.129.12 9	✓
SAL_CA6715AA	49744	SRR1957853	2014	9	23	Europe	United Kingdom	Enteritidis	2456 9	1.21.92.155.155.155.15 5	✓
SAL_CA6705AA	46132	SRR1957863	2014	8	29	Europe	United Kingdom	Enteritidis	2457 8	9.16.68.108.144.144.14 4	✓
SAL_CA6690AA	62560	SRR1957878	2014	9	5	Europe	United Kingdom	Enteritidis	2459 2	3.4.8.205.205.205.205	✓
SAL_CA6635AA	62551	SRR1957933	2014	9	3	Europe	United Kingdom	Enteritidis	2464 3	1.5.112.204.204.204.20 4	✓
SAL_CA6449AA	66859	SRR1958121	2014	10	24	Europe	United Kingdom	Enteritidis	2481 6	1.24.129.235.235.235.2 35	✓
SAL_CA6418AA	48243	SRR1958152	2014	9	15	Europe	United Kingdom	Enteritidis	2484 4	1.1.2.149.149.149.149	✓
SAL_CA6406AA	46128	SRR1958164	2014	8	29	Europe	United Kingdom	Enteritidis	2485 4	1.1.88.143.143.143.14 3	✓
SAL_CA6252AA	54060	SRR1958325	2014	9	25	Europe	United Kingdom	Enteritidis	2499 2	1.1.101.174.174.174.17 4	✓

SAL_CA5999AA	50150	SRR1958578	2014	9	24	Europe	United Kingdom	Enteritidis	25218	1.1.2.43.43.380.2290	✓
SAL_CA5913AA	46122	SRR1958664	2014	8	29	Europe	United Kingdom	Enteritidis	25292	1.1.87.142.142.142.142	✓
SAL_CA5850AA	80307	SRR1959222	2015	1	13	Europe	United Kingdom	Enteritidis	25345	1.1.202.526.680.735.915	✓
SAL_CA5846AA	70657	SRR1959226	2014	11	27	Europe	United Kingdom	Enteritidis	25347	1.25.140.251.251.251.251	✓
SAL_CA5734AA	73611	SRR1959386	2014	12	9	Europe	United Kingdom	Enteritidis	25442	1.1.151.268.268.268.268	✓
SAL_CA5678AA	71396	SRR1959443	2012	11	6	Europe	United Kingdom	Enteritidis	25491	1.26.144.258.258.258.258	✓
SAL_CA5654AA	68894	SRR1959468	2014	10	23	Europe	United Kingdom	Enteritidis	25510	1.1.136.244.244.244.244	✓
SAL_CA5566AA	71409	SRR1960073	2012	11	6	Europe	United Kingdom	Enteritidis	25587	1.7.146.262.262.262.262	✓
SAL_CA5507AA	78695	SRR1960166	2014	12	24	Europe	United Kingdom	Enteritidis	25635	1.1.222.100.1587.183.1.2556	✓
SAL_CA5446AA	73639	SRR1960236	2014	12	10	Europe	United Kingdom	Enteritidis	25687	1.21.152.270.270.270.270	✓
SAL_CA5334AA	69702	SRR1960378	2014	11	19	Europe	United Kingdom	Enteritidis	25786	1.1.138.247.247.247.247	✓

SAL_CA5315AA	80363	SRR1960665	2015	1	14	Europe	United Kingdom	Enteritidis	257981	1.5.205.604.822.905.1161	✓
SAL_CA5302AA	80341	SRR1960928	2015	1	13	Europe	United Kingdom	Enteritidis	258083	1.5.201.507.639.686.839	✓
SAL_CA5285AA	73535	SRR1961505	2014	9	19	Europe	United Kingdom	Enteritidis	508669	1.1.148.264.264.264.264	✓
SAL_CA5166AA	69142	SRR1963148	2014	11	13	Europe	United Kingdom	Enteritidis	259191	3.4.137.245.245.245.245	✓
SAL_CA5161AA	70664	SRR1963220	2014	11	27	Europe	United Kingdom	Enteritidis	259222	3.4.141.253.253.253.253	✓
SAL_CA5118AA	70666	SRR1963269	2014	11	27	Europe	United Kingdom	Enteritidis	259555	1.1.105.178.254.254.254	✓
SAL_CA4968AA	73554	SRR1963454	2014	9	22	Europe	United Kingdom	Enteritidis	260777	1.1.150.266.266.266.266	✓
SAL_CA4588AA	32527	SRR1965330	2014	7	23	Europe	United Kingdom	Enteritidis	264055	1.1.53.76.76.76.76	✓
SAL_CA4559AA	45606	SRR1965360	2014	9	9	Europe	United Kingdom	Enteritidis	264296	1.5.83.136.136.136.136	✓
SAL_CA4431AA	41987	SRR1965492	2014	8	27	Europe	United Kingdom	Enteritidis	265388	1.15.61.118.118.118.118	✓
SAL_CA4372AA	13360	SRR1965552	2014	4	15	Europe	United Kingdom	Enteritidis	265880	1.1.2.360.368.369.3150	✓

SAL_CA4299AA	99068	SRR1965636	2015	3	27	Europe	United Kingdom	Enteritidis	25745	1.1.204.580.786.862.1101	✓
SAL_CA4228AA	67566	SRR1965713	2014	11	11	Europe	United Kingdom	Enteritidis	26712	1.1.130.237.237.237.237	✓
SAL_CA4214AA	68636	SRR1965729	2014	10	13	Europe	United Kingdom	Enteritidis	73177	1.2.3.38.38.38.544	✓
SAL_CA4168AA	53007	SRR1965781	2014	10	1	Europe	United Kingdom	Enteritidis	26765	8.14.59.168.168.168.168	✓
SAL_CA4045AA	68692	SRR1965912	2014	11	12	Europe	United Kingdom	Enteritidis	26868	1.1.134.242.242.242.242	✓
SAL_CA4020AA	96239	SRR1965938	2015	3	16	Europe	United Kingdom	Enteritidis	26890	1.1.208.623.859.955.1226	✓
SAL_CA4010AA	9245	SRR1965948	2014	4	23	Europe	United Kingdom	Enteritidis	26899	1.2.3.38.38.38.1098	✓
SAL_CA3995AA	83318	SRR1965963	2015	1	21	Europe	United Kingdom	Enteritidis	26913	4.31.193.423.488.506.568	✓
SAL_CA3908AA	55582	SRR1966056	2014	9	19	Europe	United Kingdom	Enteritidis	26991	3.4.104.177.177.177.177	✓
SAL_CA3880AA	14875	SRR1966084	2014	5	20	Europe	United Kingdom	Enteritidis	27017	1.7.14.16.16.16.16	✓
SAL_CA3771AA	9286	SRR1966195	2014	5	1	Europe	United Kingdom	Enteritidis	27109	1.1.1.1.1.1.1	✓
SAL_CA3761AA	9464	SRR1966205	2014	4	29	Europe	United	Enteritidis	27191	1.1.4.9.9.9.9	✓

							King dom		19		
SAL_CA3373AA	51262	SRR1966595	2014	9	17	Europe	United King dom	Enteritidis	2748	1.1.2.167.167.167	✓
SAL_CA3359AA	83588	SRR1966609	2015	1	27	Europe	United King dom	Enteritidis	2748	1.1.198.484.603.644.780	✓
SAL_CA3248AA	65019	SRR1966723	2014	11	4	Europe	United King dom	Enteritidis	2757	1.1.124.226.226.226.226	✓
SAL_CA3045AA	38414	SRR1966926	2014	8	6	Europe	United King dom	Enteritidis	2775	1.12.64.98.98.98.98	✓
SAL_CA2965AA	73223	SRR1967006	2014	12	10	Europe	United King dom	Enteritidis	2782	1.1.147.263.263.263.263	✓
SAL_CA2952AA	63914	SRR1967019	2014	11	5	Europe	United King dom	Enteritidis	2783	1.1.119.217.217.217.217	✓
SAL_CA2914AA	12185	SRR1967057	2014	5	13	Europe	United King dom	Enteritidis	2786	1.5.9.11.11.11.11.11	✓
SAL_CA2838AA	68690	SRR1967133	2014	11	12	Europe	United King dom	Enteritidis	2792	1.1.2.240.240.240.240	✓
SAL_CA2661AA	38415	SRR1967310	2014	8	6	Europe	United King dom	Enteritidis	2807	1.1.30.99.99.99.99	✓
SAL_CA2636AA	14895	SRR1967335	2014	5	21	Europe	United King dom	Enteritidis	2810	4.8.15.17.17.17.17	✓
SAL_CA2445AA	9182	SRR1967526	2014	5	7	Europe	United King dom	Enteritidis	2820	1.2.3.18.278.278.278	✓

SAL_CA2190AA	7410	SRR1967781	2014	4	29	Europe	United Kingdom	Enteritidis	284926	1.1.157.276.276.276.276	✓
SAL_CA1919AA	65407	SRR1967973	2014	9	17	Europe	United Kingdom	Enteritidis	286613	1.1.127.233.233.233.233	✓
SAL_CA1781AA	95017	SRR1968045	2015	3	11	Europe	United Kingdom	Enteritidis	287233	1.1.212.724.1061.1193.1591	✓
SAL_CA1709AA	45579	SRR1968089	2014	9	9	Europe	United Kingdom	Enteritidis	287626	1.11.82.135.135.135.135	✓
SAL_CA1644AA	9263	SRR1968125	2014	4	24	Europe	United Kingdom	Enteritidis	288825	1.5.159.280.280.280.280	✓
SAL_CA1631AA	34201	SRR1968131	2014	7	29	Europe	United Kingdom	Enteritidis	288838	3.4.8.81.81.81.81	✓
SAL_CA1499AA	38412	SRR1968202	2014	8	6	Europe	United Kingdom	Enteritidis	289559	1.1.63.97.97.97.97	✓
SAL_CA1480AA	31651	SRR1968212	2014	7	15	Europe	United Kingdom	Enteritidis	289776	1.1.34.74.74.74.74	✓
SAL_CA1304AA	27973	SRR1968306	2014	7	17	Europe	United Kingdom	Enteritidis	290557	1.1.44.59.59.59.59	✓
SAL_CA1186AA	40280	SRR1968399	2014	8	19	Europe	United Kingdom	Enteritidis	291411	1.5.69.111.111.111.111	✓
SAL_CA1179AA	39508	SRR1968406	2014	8	18	Europe	United Kingdom	Enteritidis	291476	1.11.48.106.106.106.106	✓

SAL_CA0914AA	23508	SRR1968511	2014	6	25	Europe	United Kingdom	Enteritidis	29244	1.1.38.47.47.47	✓
SAL_CA0512AA	37836	SRR1968725	2014	8	5	Europe	United Kingdom	Enteritidis	29580	3.13.56.93.93.93	✓
SAL_CA0496AA	40366	SRR1968732	2014	8	28	Europe	United Kingdom	Enteritidis	29594	1.5.72.115.115.115.115	✓
SAL_CA0475AA	34191	SRR1968743	2014	7	29	Europe	United Kingdom	Enteritidis	29609	1.12.55.79.79.79.79	✓
SAL_CA0411AA	68689	SRR1968780	2014	11	12	Europe	United Kingdom	Enteritidis	29663	1.1.131.239.239.239.239	✓
SAL_BA9681AA	83706	SRR1969162	2014	12	4	Europe	United Kingdom	Enteritidis	25680	1.5.192.373.396.403.786	✓
SAL_BA9491AA	68696	SRR1969258	2014	11	13	Europe	United Kingdom	Enteritidis	25666	1.1.135.243.243.243.243	✓
SAL_BA9456AA	63932	SRR1969284	2014	11	6	Europe	United Kingdom	Enteritidis	30418	1.1.122.221.221.221.221	✓
SAL_BA9448AA	12110	SRR1969291	2014	5	8	Europe	United Kingdom	Enteritidis	30426	1.2.3.38.38.38.949	✓
SAL_BA9347AA	13413	SRR1969390	2014	5	16	Europe	United Kingdom	Enteritidis	30510	1.2.3.151.151.151.3167	✓
SAL_BA9112AA	45610	SRR1969527	2014	9	9	Europe	United Kingdom	Enteritidis	30712	1.1.2.137.137.137.137	✓

SAL_BA8867AA	85758	SRR1969589	2015	2	9	Europe	United Kingdom	Enteritidis	27533	1.1.200.491.619.660.802	✓
SAL_BA8861AA	6446	SRR1969592	2014	4	17	Europe	United Kingdom	Enteritidis	30900	1.1.156.275.275.275.275	✓
SAL_BA8735AA	53129	SRR1969657	2014	9	29	Europe	United Kingdom	Enteritidis	31001	1.1.2.173.173.173.173	✓
SAL_BA8599AA	39476	SRR1969727	2014	8	15	Europe	United Kingdom	Enteritidis	31119	1.11.67.104.104.104.104	✓
SAL_BA8493AA	94103	SRR1969779	2015	3	5	Europe	United Kingdom	Enteritidis	31207	1.5.209.638.889.994.1289	✓
SAL_BA8372AA	53113	SRR1969841	2014	9	29	Europe	United Kingdom	Enteritidis	31296	1.1.99.172.172.172.172	✓
SAL_BA7987AA	40348	SRR1970029	2014	8	28	Europe	United Kingdom	Enteritidis	31527	3.17.71.114.114.114.114	✓
SAL_BA7790AA	32392	SRR1970131	2014	7	25	Europe	United Kingdom	Enteritidis	31656	1.1.52.75.75.75.75	✓
SAL_BA7768AA	63923	SRR1970142	2014	11	6	Europe	United Kingdom	Enteritidis	31669	8.23.121.220.220.220.220	✓
SAL_BA7739AA	95025	SRR1970156	2015	3	11	Europe	United Kingdom	Enteritidis	31680	17.38.223.1020.1637.1891.2642	✓
SAL_EA7787AA	21091	SRR3048975	2014	6	3	Europe	United Kingdom	Enteritidis	70669	1.11.31.37.37.37.37	✓
SAL_EA7715AA	99074	SRR3049054	2014	3	27	Europe	United	Enteritidis	7 1	15.32.196.474.586.621.745	✓

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SAL_ EA77 08AA	209 03	SRR30 49061	2014	6	5	Eur ope	Unit ed King dom	Ent erit idis	71 46	1.1.26.31.3 1.31.31	✓
SAL_ EA75 29AA	185 77	SRR30 49240	2014	6	6	Eur ope	Unit ed King dom	Ent erit idis	73 19	4.9.21.24.2 4.24.24	✓
SAL_ EA75 24AA	299 60	SRR30 49245	2014	7	23	Eur ope	Unit ed King dom	Ent erit idis	73 24	1.1.191.358 .363.364.36 6	✓
SAL_ EA74 20AA	530 76	SRR30 49354	2014	9	30	Eur ope	Unit ed King dom	Ent erit idis	74 24	1.1.98.171. 171.171.17 1	✓
SAL_ EA74 07AA	185 31	SRR30 49367	2014	6	4	Eur ope	Unit ed King dom	Ent erit idis	74 36	1.1.229.103 4.1684.195 4.2823	✓
SAL_ EA70 45AA	210 65	SRR30 49778	2014	6	3	Eur ope	Unit ed King dom	Ent erit idis	77 75	1.10.28.33. 33.33.33	✓
SAL_ FA39 83AA	185 901	SRR32 84689	2015	11	3	Eur ope	Unit ed King dom	Ent erit idis	19 57	1.1.242.106 5.1746.205 1.3585	✓
SAL_ FA39 63AA	166 245	SRR32 84721	2015	9	23	Eur ope	Unit ed King dom	Ent erit idis	19 76	1.2.270.114 5.1898.226 4.3626	✓
SAL_ FA39 48AA	134 013	SRR32 84736	2015	7	15	Eur ope	Unit ed King dom	Ent erit idis	19 89	1.1.245.107 0.1756.206 3.3141	✓
SAL_ FA39 13AA	197 074	SRR32 84773	2015	12	4	Eur ope	Unit ed King dom	Ent erit idis	20 21	1.1.47.214. 1658.2500. 4224	✓
SAL_ FA38 44AA	183 662	SRR32 85109	2015	10	27	Eur ope	Unit ed King dom	Ent erit idis	20 80	1.1.228.103 3.1681.194 6.4002	✓
SAL_ FA38 40AA	206 728	SRR32 85244	2016	1	12	Eur ope	Unit ed King dom	Ent erit idis	20 84	1.1.2.197.5 44.2403.43 25	✓
SAL_ FA38 31AA	133 214	SRR32 85283	2015	7	14	Eur ope	Unit ed King dom	Ent erit idis	20 92	1.1.2.1066. 1749.2054. 3119	✓
SAL_ FA37 55AA	146 116	SRR32 85416	2015	8	12	Eur ope	Unit ed	Ent erit idis	21	1.3.249.108 2.1788.211 3.3276	✓

							King dom		56		
SAL_FA37 10AA	180 813	SRR32 85462	2015	9	10	Europe	United King dom	Enterit idis	219 6	1.2.262.113 7.1888.225 4.3602	✓
SAL_FA37 02AA	170 334	SRR32 85470	2015	9	17	Europe	United King dom	Enterit idis	220 3	1.27.225.11 50.1907.22 77.3665	✓
SAL_FA36 34AA	104 253	SRR32 86602	2015	4	20	Europe	United King dom	Enterit idis	226 2	1.3.224.102 1.1652.190 6.2677	✓
SAL_FA35 09AA	122 682	SRR32 86836	2015	6	12	Europe	United King dom	Enterit idis	236 7	1.1.236.104 9.1714.199 8.2934	✓
SAL_FA34 91AA	122 699	SRR32 86863	2015	6	15	Europe	United King dom	Enterit idis	237 81	1.1.237.105 1.1716.200 1.2940	✓
SAL_FA34 87AA	120 575	SRR32 86870	2015	4	30	Europe	United King dom	Enterit idis	234 85	1.1.234.104 5.1708.198 2.2900	✓
SAL_FA34 79AA	119 502	SRR32 86886	2015	6	2	Europe	United King dom	Enterit idis	233 92	1.1.233.104 4.1704.197 6.2889	✓
SAL_FA73 30AA	143 553	SRR35 85347	2015	8	10	Europe	United King dom	Enterit idis	402 53	1.1.250.108 5.1794.212 2.3293	✓
SAL_FA73 29AA	152 413	SRR35 85348	2015	8	25	Europe	United King dom	Enterit idis	402 54	1.1.256.110 1.1827.216 5.3375	✓
SAL_FA73 27AA	164 715	SRR35 85351	2015	9	21	Europe	United King dom	Enterit idis	402 56	1.3.263.112 8.1873.222 9.3531	✓
SAL_FA73 26AA	134 034	SRR35 85352	2015	7	8	Europe	United King dom	Enterit idis	402 57	1.1.242.106 5.1746.205 1.3115	✓
SAL_FA73 25AA	137 147	SRR35 85354	2015	7	23	Europe	United King dom	Enterit idis	402 58	4.44.246.10 71.1757.20 64.3146	✓

SAL_FA7324AA	179844	SRR3585355	2015	10	23	Europe	United Kingdom	Enteritidis	40259	1.1.277.1177.1995.2391.3912	✓
SAL_FA7323AA	154869	SRR3585356	2015	9	1	Europe	United Kingdom	Enteritidis	40260	1.47.260.1114.1845.2190.3444	✓
SAL_FA7322AA	120578	SRR3585357	2015	6	2	Europe	United Kingdom	Enteritidis	40261	1.3.235.1046.1710.1985.2905	✓
SAL_FA7321AA	153189	SRR3585358	2015	8	27	Europe	United Kingdom	Enteritidis	40262	4.45.257.1106.1833.2173.3394	✓
SAL_FA7320AA	160846	SRR3585359	2015	9	14	Europe	United Kingdom	Enteritidis	40263	4.31.264.1129.1875.2231.3537	✓
SAL_FA7319AA	160806	SRR3585360	2015	9	10	Europe	United Kingdom	Enteritidis	40264	1.2.262.1118.1850.2199.3462	✓
SAL_FA7318AA	131456	SRR3585361	2015	7	8	Europe	United Kingdom	Enteritidis	40265	3.4.241.1063.1740.2047.2308	✓
SAL_FA7317AA	178732	SRR3585363	2015	10	13	Europe	United Kingdom	Enteritidis	40266	1.5.276.1175.1987.2378.3879	✓
SAL_FA7316AA	183605	SRR3585364	2015	11	2	Europe	United Kingdom	Enteritidis	40267	1.5.279.1188.2016.2426.4013	✓
SAL_FA7315AA	190569	SRR3585365	2015	11	24	Europe	United Kingdom	Enteritidis	40268	20.53.283.1206.2050.2481.4147	✓
SAL_FA7314AA	185894	SRR3585367	2015	11	11	Europe	United Kingdom	Enteritidis	40269	1.1.280.1189.2017.2431.4023	✓

SAL_FA7313AA	168519	SRR3585375	2015	9	25	Europe	United Kingdom	Enteritidis	4027	4.50.271.1154.1912.2284.3677	✓
SAL_FA7312AA	110976	SRR3585376	2015	5	11	Europe	United Kingdom	Enteritidis	2345	1.1.228.1033.1681.1946.2785	✓
SAL_FA7311AA	193289	SRR3585377	2015	12	2	Europe	United Kingdom	Enteritidis	4027	13.52.281.1202.2042.2470.4123	✓

List of the 8965 *Salmonella* serovar Enteritidis isolates used in Chapter Three

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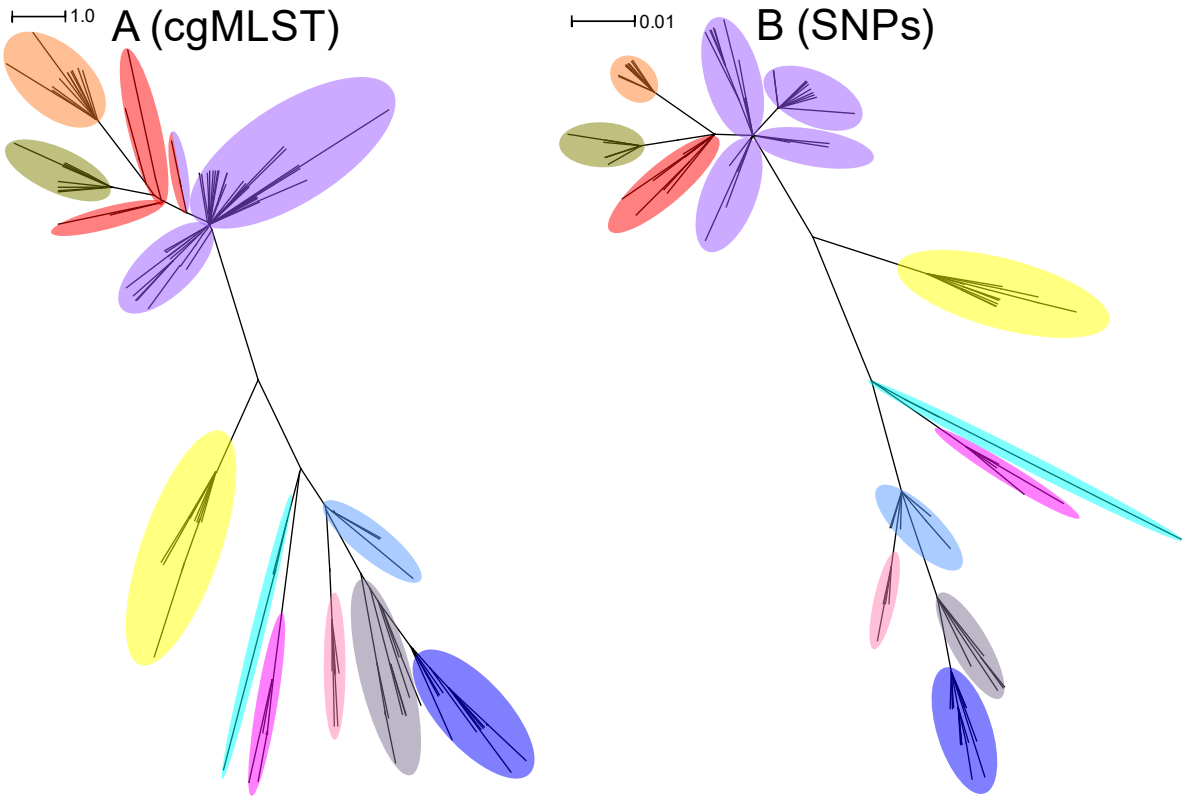
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SAL_HA0665AA SAL_HA0671AA SAL_HA0696AA SAL_HA0697AA SAL_HA0698AA SAL_HA0699AA
SAL_HA0700AA SAL_HA0701AA SAL_HA0702AA SAL_HA0703AA SAL_HA0704AA SAL_HA0705AA
SAL_HA0726AA SAL_HA0729AA SAL_HA0738AA SAL_HA0739AA SAL_HA0740AA SAL_HA0741AA
SAL_HA0752AA SAL_HA0764AA SAL_HA0765AA SAL_HA0766AA SAL_HA0777AA SAL_HA0841AA
SAL_HA0862AA SAL_HA0863AA SAL_HA0865AA SAL_HA0866AA SAL_HA0868AA SAL_HA0873AA
SAL_HA0874AA SAL_HA0884AA SAL_HA0891AA SAL_HA0906AA SAL_HA0926AA SAL_HA0937AA



Core genome neighbour-joining tree (A) and single nucleotide polymorphism neighbour-joining tree (B).

A: neighbour-joining tree of the 386 isolates used to create the Tanglegram (Fig. 1) calculated using the cgMLST scheme which consists of 3002 loci and is available in the EnteroBase database. The tree was drawn using SplitsTree4 (Huson and Bryant, 2006).

B: neighbour-joining tree of the 386 isolates used to create the Tanglegram (Fig. 1) calculated using the PHE SNP pipeline. The tree was drawn using SplitsTree4 (Huson and Bryant, 2006).

The trees, drawn within SplitsTree4 (Huson and Bryant, 2006) were coloured based on closely related groups of isolates. The overall topology of the trees and the majority of the clusters demonstrated strong congruence between SNP and cgMLST based approaches. Minor differences were observed, such as the purple group was split into four clusters via SNPs and only two via cgMLST, none of which were directly congruent between the two methods. However, all isolates within the purple clusters were more closely related to each other than their neighbours. There were also two isolates, split into the red and purple groups by SNPs, which were very closely related via cgMLST. Despite these exceptions the rest of the isolates fell into highly congruent clusters, which suggested strong similarities between the two methods.

Appendix D

Table showing all of the isolates used within the analyses

All of the isolates included within the analyses matched both metadata and phylogenetic clustering, with the exception of one isolate belonging to subspecies II, from PHE where further investigations still typed it as a subspecies II despite it clustering with subspecies I phylogenetically. All of these isolates were available from both Enterobase and PubMLST (at time of analysis).

Pubmlst_Salmonella_id	Analysis_Subspecies	Structure_Analysis
12318	I	Yes
13447	I	Yes
13393	I	Yes
12766	I	Yes
14862	I	Yes
13034	I	Yes
13839	I	
12121	I	
12955	I	
13250	I	
13526	I	
13441	I	
14489	I	
11887	I	
14751	I	
12380	I	
12939	I	
14746	I	
11494	I	
12918	I	
14387	I	
11919	I	
11891	I	
11483	I	
3709	I	
11791	I	
3592	I	
11800	I	
13675	I	
12418	I	
12004	I	
12303	I	
13490	I	
12255	I	
14148	I	
13146	I	
3605	I	
11608	I	

Pubmlst_Salmonella_id	Analysis_Subspecies	Structure_Analysis
16820	IIIa	
16817	IIIa	
16825	IIIa	
16281	IIIa	
16830	IIIa	
16841	IIIa	
16840	IIIa	
16839	IIIa	
16847	IIIa	
16850	IIIa	
16856	IIIa	
16869	IIIa	
16871	IIIa	
16880	IIIa	
16878	IIIa	
16887	IIIa	
16889	IIIa	
16987	IIIa	
16988	IIIa	
16985	IIIa	
16984	IIIa	
16979	IIIa	
16978	IIIa	
16135	IIIa	
16975	IIIa	
16974	IIIa	
16291	IIIa	
16972	IIIa	
16971	IIIa	
16966	IIIa	
16965	IIIa	
16963	IIIa	
16960	IIIa	
16959	IIIa	
16958	IIIa	
16957	IIIa	
16956	IIIa	
16955	IIIa	

13637	I
11997	I
14864	I
14114	I
13670	I
14276	I
3617	I
13547	I
3673	I
14254	I
14177	I
13650	I
13468	I
3684	I
13501	I
13099	I
12359	I
13987	I
14865	I
15328	I
14093	I
13509	I
11469	I
11794	I
15161	I
11670	I
11474	I
13752	I
14153	I
14925	I
11484	I
11839	I
13234	I
14460	I
14866	I
11481	I
12371	I
11584	I
12015	I
12130	I
11642	I
13999	I
12232	I
12218	I
15326	I
11633	I
14504	I
11607	I

16954	IIIa
16953	IIIa
16945	IIIa
16942	IIIa
16941	IIIa
16940	IIIa
16299	IIIa
16936	IIIa
16935	IIIa
16929	IIIa
16926	IIIa
16924	IIIa
16922	IIIa
16921	IIIa
16917	IIIa
16915	IIIa
16913	IIIa
16907	IIIa
16905	IIIa
16904	IIIa
16898	IIIa
16894	IIIa
16316	IIIa
17016	IIIa
17015	IIIa
16039	IIIa
17013	IIIa
17010	IIIa
17006	IIIa
17004	IIIa
17000	IIIa
16999	IIIa
16995	IIIa
16994	IIIa
16990	IIIa
17025	IIIa
17038	IIIa
17036	IIIa
17035	IIIa
16326	IIIa
17029	IIIa
17026	IIIa
16031	IIIa
17046	IIIa
17044	IIIa
17042	IIIa
17049	IIIa
17063	IIIa

3586	I		15999	IIIa
14368	I		17094	IIIa
13832	I		17122	IIIa
11473	I		15975	IIIa
13640	I		17130	IIIa
11851	I		17139	IIIa
13667	I		16361	IIIa
12283	I		17148	IIIa
12925	I		17167	IIIa
13517	I		17169	IIIa
3689	I		16368	IIIa
14509	I		17171	IIIa
3635	I		17177	IIIa
3757	I		11643	IIIb	Yes
12952	I		12465	IIIb	Yes
13627	I		16789	IIIb	Yes
14910	I		16986	IIIb	Yes
14223	I		16024	IIIb	Yes
13625	I		17156	IIIb	Yes
11721	I		17160	IIIb	Yes
14867	I		13476	IIIb	
3723	I		13065	IIIb	
14463	I		13482	IIIb	
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11471	I		13545	IIIb	
14200	I		13544	IIIb	
14039	I		13543	IIIb	
13553	I		14921	IIIb	
11882	I		14919	IIIb	
14697	I		12963	IIIb	
16116	I		13585	IIIb	
12214	I		12250	IIIb	
13555	I		16420	IIIb	
11897	I		12207	IIIb	
3587	I		16428	IIIb	
13996	I		16429	IIIb	
12235	I		11933	IIIb	
14074	I		16431	IIIb	
13580	I		16432	IIIb	
14386	I		16433	IIIb	
12262	I		12028	IIIb	
12354	I		11733	IIIb	
3735	I		15348	IIIb	
3664	I		16440	IIIb	
11874	I		16441	IIIb	
13581	I		16442	IIIb	
13550	I		11973	IIIb	
3756	I		16443	IIIb	

14471	I	16445	IIIb
13507	I	11704	IIIb
11582	I	16447	IIIb
11888	I	11517	IIIb
12306	I	16450	IIIb
14052	I	12006	IIIb
14750	I	11783	IIIb
13129	I	11873	IIIb
14297	I	11631	IIIb
11617	I	16417	IIIb
11777	I	12397	IIIb
12131	I	12222	IIIb
14439	I	11745	IIIb
11604	I	16456	IIIb
3588	I	16416	IIIb
13974	I	16459	IIIb
14527	I	12027	IIIb
12280	I	16425	IIIb
11730	I	16464	IIIb
13576	I	16466	IIIb
3623	I	11912	IIIb
14484	I	11711	IIIb
3654	I	16473	IIIb
14209	I	16475	IIIb
12669	I	16477	IIIb
11916	I	16482	IIIb
12259	I	16526	IIIb
12081	I	16421	IIIb
14977	I	16483	IIIb
11786	I	11765	IIIb
13277	I	16484	IIIb
14239	I	12069	IIIb
13092	I	13422	IIIb
11852	I	15375	IIIb
13689	I	14522	IIIb
12970	I	14530	IIIb
14302	I	14483	IIIb
13530	I	14508	IIIb
13426	I	14529	IIIb
12201	I	14511	IIIb
14355	I	14521	IIIb
14198	I	14526	IIIb
13442	I	14520	IIIb
13515	I	14518	IIIb
12921	I	14524	IIIb
13383	I	14510	IIIb
13105	I	15117	IIIb
11658	I	14830	IIIb

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12120	I
14748	I
14775	I
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14887	I
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13241	I
14260	I
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3638	I
12186	I
11707	I
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16179	I
15355	I
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16516	IIIb
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13273	IIIb
13995	IIIb
13991	IIIb
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14137	IIIb
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15292	IIIb
15288	IIIb
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14787	IIIb
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16544	IIIb
12048	IIIb

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3613	I
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14566	I
11962	I
12610	I
3639	I
14818	I
11986	I

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13593	IIIb
16214	IIIb
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15400	IIIb
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16586	IIIb
16584	IIIb
16583	IIIb
16566	IIIb
16565	IIIb
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12715	IIIb
12485	IIIb
12486	IIIb
16232	IIIb
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12840	IIIb
16589	IIIb
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16596	IIIb
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16605	IIIb
16234	IIIb
16604	IIIb
16603	IIIb
16602	IIIb
16601	IIIb
16235	IIIb
16236	IIIb
16625	IIIb
16617	IIIb

3710	I	16620	IIIb
12134	I	16244	IIIb
13479	I	16652	IIIb
3603	I	16633	IIIb
13411	I	16245	IIIb
14805	I	16631	IIIb
12070	I	16246	IIIb
3648	I	16248	IIIb
11751	I	16250	IIIb
13237	I	16628	IIIb
14047	I	16627	IIIb
14298	I	16650	IIIb
12054	I	16648	IIIb
14183	I	16643	IIIb
12108	I	16661	IIIb
12044	I	16253	IIIb
12058	I	16653	IIIb
14115	I	16665	IIIb
13329	I	16390	IIIb
12230	I	16373	IIIb
12265	I	16389	IIIb
14035	I	16404	IIIb
14028	I	16680	IIIb
3743	I	16694	IIIb
14890	I	16701	IIIb
14056	I	16705	IIIb
13247	I	16704	IIIb
12148	I	16712	IIIb
14797	I	16717	IIIb
11708	I	16729	IIIb
12111	I	16728	IIIb
12183	I	16727	IIIb
13508	I	16726	IIIb
12317	I	16725	IIIb
13284	I	16724	IIIb
12292	I	16723	IIIb
13835	I	16722	IIIb
12383	I	16719	IIIb
13483	I	16732	IIIb
14874	I	16731	IIIb
14792	I	16735	IIIb
14875	I	16082	IIIb
13425	I	16739	IIIb
11910	I	16086	IIIb
13612	I	16741	IIIb
13340	I	16745	IIIb
11576	I	16758	IIIb
11599	I	16755	IIIb

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12276	I			16753	IIIb
14455	I			16805	IIIb
12005	I			16804	IIIb
13748	I			16802	IIIb
13289	I			16801	IIIb
14108	I			16799	IIIb
13233	I			16797	IIIb
11600	I			16794	IIIb
13639	I			16793	IIIb
11797	I			16792	IIIb
11892	I	Yes		16790	IIIb
13989	I			16786	IIIb
13988	I			16784	IIIb
13572	I			16783	IIIb
14025	I			16782	IIIb
13360	I			16778	IIIb
13571	I			16811	IIIb
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11727	I			16862	IIIb
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16455	IIIa	Yes		16034	IV
16136	IIIa	Yes		16032	IV
13863	IIIa	Yes		17045	IV
16768	IIIa	Yes		17041	IV
16977	IIIa	Yes		17082	IV
17113	IIIa	Yes		17119	IV
17159	IIIa	Yes		15978	IV
13162	IIIa			16354	IV
16165	IIIa			15976	IV
16166	IIIa			16355	IV
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16435	IIIa			17127	IV
16422	IIIa			17128	IV
16519	IIIa			16357	IV
14920	IIIa			15974	IV
15347	IIIa			15970	IV
16446	IIIa			17136	IV
16451	IIIa			16360	IV
16410	IIIa			15968	IV

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11635	IIIa		17150	IV	
16458	IIIa		17153	IV	
11601	IIIa		15977	IV	
16460	IIIa		16139	IV	
16463	IIIa		16365	IV	
16467	IIIa		15959	IV	
16470	IIIa		15958	IV	
16478	IIIa		17164	IV	
16418	IIIa		17163	IV	
16480	IIIa		17161	IV	
16481	IIIa		17168	IV	
12084	IIIa		16141	novel_subspecies_A	Yes
16488	IIIa		16142	novel_subspecies_A	Yes
16492	IIIa		16111	novel_subspecies_A	Yes
11853	IIIa		13568	novel_subspecies_B	Yes
13607	IIIa		16658	novel_subspecies_B	Yes
15367	IIIa		16664	novel_subspecies_B	Yes
15376	IIIa		16756	novel_subspecies_B	Yes
15377	IIIa		16156	novel_subspecies_B	Yes
13460	IIIa		15996	novel_subspecies_B	Yes
16411	IIIa		17115	novel_subspecies_B	Yes
13919	IIIa		15280	novel_subspecies_B	
13665	IIIa		16155	novel_subspecies_B	
13918	IIIa		13316	novel_subspecies_B	
13915	IIIa		16143	novel_subspecies_B	
13913	IIIa		16158	novel_subspecies_B	
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13914	IIIa		16660	novel_subspecies_B	
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15374	IIIa		16663	novel_subspecies_B	
13907	IIIa		16669	novel_subspecies_B	

13908	IIIa	16157	novel_subspecies_B
13909	IIIa	16668	novel_subspecies_B
13912	IIIa	16667	novel_subspecies_B
13630	IIIa	16666	novel_subspecies_B
14448	IIIa	16671	novel_subspecies_B
14380	IIIa	16670	novel_subspecies_B
14369	IIIa	16679	novel_subspecies_B
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15368	IIIa	16688	novel_subspecies_B
12535	IIIa	16697	novel_subspecies_B
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14614	IIIa	16720	novel_subspecies_B
12828	IIIa	16730	novel_subspecies_B
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13229	IIIa	16791	novel_subspecies_B
12886	IIIa	16858	novel_subspecies_B
16506	IIIa	16859	novel_subspecies_B
16409	IIIa	17024	novel_subspecies_B
16512	IIIa	17095	novel_subspecies_B
12623	IIIa	16153	novel_subspecies_B
16513	IIIa	15979	novel_subspecies_B
15360	IIIa	17114	novel_subspecies_B
12817	IIIa	17117	novel_subspecies_B
15359	IIIa	17116	novel_subspecies_B
13961	IIIa	17118	novel_subspecies_B
15396	IIIa	17120	novel_subspecies_B

13268	IIIa	17121	novel_subspecies_B	
13904	IIIa	17187	novel_subspecies_B	
13903	IIIa	17188	novel_subspecies_B	
15395	IIIa	16521	novel_subspecies_C	Yes
14122	IIIa	9629	novel_subspecies_C	Yes
13972	IIIa	16159	novel_subspecies_C	Yes
15392	IIIa	12478	novel_subspecies_C	Yes
16106	IIIa	12469	novel_subspecies_C	Yes
13246	IIIa	16686	novel_subspecies_C	Yes
13965	IIIa	16161	novel_subspecies_C	Yes
14926	IIIa	16145	novel_subspecies_C	
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13136	IIIa	16080	novel_subspecies_C	
15384	IIIa	16160	novel_subspecies_C	
15386	IIIa	17108	novel_subspecies_C	
15385	IIIa	15989	novel_subspecies_C	
15387	IIIa	17112	novel_subspecies_C	
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16517	IIIa	15967	novel_subspecies_C	
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15018	IIIa	16162	novel_subspecies_C	
16529	IIIa	16415	*S.bongori*	Yes
15334	IIIa	13799	*S.bongori*	Yes
16530	IIIa	16570	*S.bongori*	Yes
16533	IIIa	16095	*S.bongori*	Yes
16535	IIIa	16090	*S.bongori*	Yes
16536	IIIa	16267	*S.bongori*	Yes
16540	IIIa	16362	*S.bongori*	Yes
16547	IIIa	12139	*S.bongori*	
15146	IIIa	12049	*S.bongori*	
15151	IIIa	15140	*S.bongori*	
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12325	IIIa		16493	*S.bongori*	
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13446	IIIa		16499	*S.bongori*	
13595	IIIa		16500	*S.bongori*	
16217	IIIa		16501	*S.bongori*	
16598	IIIa		16502	*S.bongori*	
16594	IIIa		16503	*S.bongori*	
16588	IIIa		13189	*S.bongori*	
12855	IIIa		13269	*S.bongori*	
14906	IIIa		16206	*S.bongori*	
14905	IIIa		16548	*S.bongori*	
12852	IIIa		16549	*S.bongori*	
12850	IIIa		14904	*S.bongori*	
12838	IIIa		16587	*S.bongori*	
16582	IIIa		16221	*S.bongori*	
16580	IIIa		16100	*S.bongori*	
16574	IIIa		16222	*S.bongori*	
12853	IIIa		16223	*S.bongori*	
14903	IIIa		16109	*S.bongori*	
14902	IIIa		16224	*S.bongori*	
16573	IIIa		16225	*S.bongori*	
12851	IIIa		16110	*S.bongori*	
12755	IIIa		16572	*S.bongori*	
12648	IIIa		16569	*S.bongori*	
12630	IIIa		16614	*S.bongori*	
12839	IIIa		16392	*S.bongori*	
12837	IIIa		16265	*S.bongori*	
16592	IIIa		16765	*S.bongori*	
16595	IIIa		16762	*S.bongori*	
16237	IIIa		16269	*S.bongori*	
16609	IIIa		16274	*S.bongori*	
16610	IIIa		16771	*S.bongori*	
16616	IIIa		16814	*S.bongori*	
16615	IIIa		16812	*S.bongori*	
16101	IIIa		16021	*S.bongori*	
16619	IIIa		17086	*S.bongori*	
16621	IIIa		16353	*S.bongori*	
16622	IIIa		15972	*S.bongori*	
16247	IIIa		16358	*S.bongori*	
16249	IIIa		15971	*S.bongori*	
16098	IIIa		17135	*S.bongori*	
16632	IIIa		17138	*S.bongori*	
16630	IIIa		17142	*S.bongori*	
16629	IIIa		13620	VI	Yes
16644	IIIa		12496	VI	Yes
16655	IIIa		12476	VI	Yes

16657	IIIa		16220	VI	Yes
16395	IIIa		12601	VI	Yes
16396	IIIa		16393	VI	Yes
16397	IIIa		16767	VI	Yes
16398	IIIa		11463	VI	
16399	IIIa		14197	VI	
16400	IIIa		14055	VI	
16401	IIIa		12479	VI	
16403	IIIa		16152	VI	
16406	IIIa		12645	VI	
16672	IIIa		12633	VI	
16676	IIIa		16151	VI	
16675	IIIa		16579	VI	
16681	IIIa		16578	VI	
16690	IIIa		12470	VI	
16691	IIIa		12603	VI	
16693	IIIa		12605	VI	
16695	IIIa		12750	VI	
16700	IIIa		12848	VI	
16702	IIIa		16092	VI	
16708	IIIa		16766	VI	
16711	IIIa		16268	VI	
16714	IIIa		16827	VI	
16733	IIIa		16964	VI	
16097	IIIa		17137	VI	
16088	IIIa		15147	VII	Yes
16740	IIIa		13892	VII	Yes
16744	IIIa		16552	VII	Yes
16750	IIIa		12609	VII	Yes
16763	IIIa		16163	VII	Yes
16760	IIIa		16164	VII	Yes
16752	IIIa		16108	VII	Yes
16751	IIIa		13894	VII	
16807	IIIa		17178	VII	
16806	IIIa		17179	VII	
16803	IIIa		16577	VII	
16798	IIIa		12664	VII	
16079	IIIa		17180	VII	
16078	IIIa		17181	VII	
16273	IIIa		17182	VII	
16780	IIIa		17183	VII	
16779	IIIa		17184	VII	
16777	IIIa		16883	VII	
16776	IIIa		16885	VII	
16773	IIIa		17185	VII	
16809	IIIa		17186	VII	
16815	IIIa		17162	VII	
16821	IIIa				

Appendix E

Table showing the isolates removed from the analyses and the reasons why they were removed.

Isolates were predominantly removed due to discrepancies between their metadata and which subspecies the isolate clustered with phylogenetically. This incongruence between the two approaches meant that isolates were removed to avoid possible discrepancies in the creation of the scheme.

Column1	Column2	Column3	Column4	Column5
Enterobase_Barcode	Enterobase_Name	Accession_No.	Metadata_Subspecies	Reason_removed
SAL_GA3753AA	3940-62	SRR1060612	II	Clustered_with_IIIb
SAL_BA4685AA	CFSAN006231	SRR965139	II	Clustered_with_I
SAL_BA3523AA	CFSAN024501	SRR2054210	II	Clustered_with_I
SAL_BA3526AA	CFSAN024542	SRR2054206	II	Clustered_with_I
SAL_BA3600AA	CFSAN024551	SRR2053360	II	Clustered_with_I
SAL_BA3581AA	CFSAN024557	SRR2054124	II	Clustered_with_I
SAL_BA3537AA	CFSAN024561	SRR2054195	II	Clustered_with_I
SAL_BA3576AA	CFSAN024576	SRR2054131	II	Clustered_with_I
SAL_BA5443AA	CFSAN024604	SRR2011320	II	Clustered_with_I
SAL_BA5388AA	CFSAN024614	SRR2011443	II	Clustered_with_I
SAL_DA8130AA	FAR0100	SRR1248827	II	Clustered_with_I
SAL_BA4703AA	FDA00000624	SRR2025286	II	Clustered_with_IV
SAL_GA4495AA	FDA00001404	SRR3747678	II	Clustered_with_I
SAL_FA7834AA	FDA00002751	SRR3654321	II	Clustered_with_I
SAL_BA1533AA	FDA00003428	SRR2127519	II	Clustered_with_I
SAL_CA9985AA	FDA00003681	SRR1658079	II	Clustered_with_I
SAL_EA6716AA	FDA00005031	SRR3027337	II	Clustered_with_I
SAL_DA7772AA	FMA0131	SRR1265013	II	Clustered_with_I
SAL_DA9674AA	FNW19G54	SRR1168377	II	Clustered_with_I
SAL_DA0298AA	AZ-TG74268	SRR1646584	IIIa	Clustered_with_I
SAL_DA0325AA	AZ-TG74272	SRR1646557	IIIa	Clustered_with_I
SAL_DA8127AA	FAR0092	SRR1248858	IIIa	Clustered_with_I
SAL_BA1630AA	FDA00001441	SRR2124507	IIIa	Clustered_with_IV
SAL_CA7826AA	FDA00002874	SRR1812840	IIIa	Clustered_with_I
SAL_IA0303AA	FDA00004405	SRR5182485	IIIa	Clustered_with_I
SAL_CA7208AA	FDA00008857	SRR1920226	IIIa	Clustered_with_IIIb
SAL_EA0007AA	FMA0015	SRR1139510	IIIa	Clustered_with_I
SAL_EA0031AA	FNE0029	SRR1107844	IIIa	Clustered_with_I
SAL_BA8917AA	NY_FSL_S10-1447	SRR6814029	IIIa	Clustered_with_IIIb
SAL_IA7710AA	S/20170031	traces-0qTxbwH	IIIa	Clustered_with_IIIb
SAL_JA1698AA	S/20170129V	traces-0ytsFjV	IIIa	Clustered_with_IIIb
SAL_NA8968AA	ADRDL-1249	SRR6667086	IIIb	Clustered_with_I
SAL_GA3870AA	BCW_1536	SRR1060729	IIIb	Clustered_with_I
SAL_GA3867AA	BCW_1540	SRR1060726	IIIb	Clustered_with_IV

SAL_BA5034AA	CFSAN024528	SRR2015650	IIIb	Clustered_with_I
SAL_GA7131AA	CFSAN044908	SRR4012677	IIIb	Clustered_with_I
SAL_GA7097AA	CFSAN044946	SRR4012810	IIIb	Clustered_with_I
SAL_GA7032AA	CFSAN045012	SRR4012883	IIIb	Clustered_with_I
SAL_GA7031AA	CFSAN045013	SRR4012884	IIIb	Clustered_with_I
SAL_GA7026AA	CFSAN045018	SRR4012889	IIIb	Clustered_with_I
SAL_GA7024AA	CFSAN045020	SRR4012891	IIIb	Clustered_with_I
SAL_GA7020AA	CFSAN045024	SRR4012895	IIIb	Clustered_with_I
SAL_GA7009AA	CFSAN045035	SRR4012912	IIIb	Clustered_with_I
SAL_GA7003AA	CFSAN045041	SRR4012921	IIIb	Clustered_with_I
SAL_OA2407AA	FDA00000390	SRR6805495	IIIb	Clustered_with_VI
SAL_DA9957AA	FNE0047	SRR1153373	IIIb	Clustered_with_I
SAL_JA4423AA	1256/72	traces-0VchwxH	IV	Clustered_with_I
SAL_GA3732AA	23-88	SRR1060591	IV	Clustered_with_II
SAL_GA1782AA	343-86	SRR1840598	IV	Clustered_with_IIIb
SAL_GA3863AA	BCW_1547	SRR1060722	IV	Clustered_with_I
SAL_DA0242AA	FDA00000194	SRR1648163	IV	Clustered_with_I
SAL_CA9659AA	FDA00003745	SRR1693404	IV	Clustered_with_I
SAL_CA9658AA	FDA00003746	SRR1693405	IV	Clustered_with_I
SAL_CA9683AA	FDA00003747	SRR1693289	IV	Clustered_with_I
SAL_CA9682AA	FDA00003748	SRR1693290	IV	Clustered_with_I
SAL_HA0111AA	FDA00004094	SRR4301130	IV	Clustered_with_I
SAL_MA7355AA	OH-17-7250	SRR6310076	IV	Clustered_with_I
SAL_GA3730AA	327-80	SRR1060589	S._bongori	Clustered_with_II
SAL_JA4410AA	194K	traces-0vgfZav	VI	Clustered_with_I
SAL_JA4401AA	3539/82	traces-0ZPviIA	VI	Clustered_with_I
SAL_EA0303AA	FSW0079	SRR1068316	VI	Clustered_with_I
SAL_CA2954AA	36981	SRR1967017	I	Misidentfied_subspecies_I_metadata_updated
SAL_NA5006AA	461962	traces-0WDfUBi	I	Misidentfied_subspecies_I_metadata_updated
SAL_NA5045AA	462004	traces-0aAwsuq	I	Misidentfied_subspecies_I_metadata_updated
SAL_BA2254AA	FDA00001203	SRR2086557	I	Clustered_with_II
SAL_BA2781AA	FDA00009159	SRR2075153	I	Clustered_with_II
SAL_BA5399AA	CFSAN024601	SRR2011437	I	Clustered_with_IV
SAL_CA7292AA	FDA00001035	SRR1917478	I	Enterobase_metadata_IV
SAL_DA1890AA	FDA00000118	SRR1633528	I	Clustered_with_VI
SAL_DA4281AA	MOD1_Sal_882	SRR1548438	I	Clustered_with_IV
SAL_DA5934AA	CFSAN018512	SRR1501690	I	Enterobase_metadata_II
SAL_DA7356AA	FSW0196	SRR1272845	I	Clustered_with_II
SAL_DA8117AA	FAR0083	SRR1248943	I	Enterobase_metadata_II
SAL_EA0576AA	FL_FLDACS-12104	SRR1041498	I	Enterobase_metadata_IIIb

Table showing the paralogous core genome loci

These loci were removed from the core genome schemes in order to perform the STRUCTURE analyses, due to the presence of paralogs in one or more isolates. The schemes from which they were removed was also stated.

loci	analysis_removed_from
STMMW_36391	Enterobase_Scheme&Genus_Scheme
STMMW_00801	Enterobase_Scheme&Genus_Scheme
STMMW_17531	Enterobase_Scheme&Genus_Scheme
STMMW_23761	Enterobase_Scheme&Genus_Scheme
STMMW_44771	Enterobase_Scheme&Genus_Scheme
STMMW_05331	Enterobase_Scheme&Genus_Scheme
STMMW_35531	Enterobase_Scheme&Genus_Scheme
STMMW_13231	Enterobase_Scheme&Genus_Scheme
STMMW_24481	Enterobase_Scheme&Genus_Scheme
STMMW_37551	Enterobase_Scheme
STMMW_18441	Enterobase_Scheme

Table showing the 252 loci to be removed from the EBcgMLSTv2.0

The loci described here were absent in over 2% of at least one of the subspecies. All of the loci were present in over 98% of subspecies I, while the non-subspecies I analyses found between 10 – 108 loci needed to be removed per subspecies. 98 of these loci met the required threshold for removal (2%) in multiple subspecies. These loci were removed from EBcgMLSTv2.0 to create the genus core genome scheme proposed here.

locus	subspecies
STMMW_11031	II
STMMW_23611	II
STMMW_23621	II
STMMW_23641	II
STMMW_23651	II
STMMW_23661	II
STMMW_23671	II
STMMW_42501	II
STMMW_43331	II
STMMW_12521	II
STMMW_12541	II
STMMW_12562	II
STMMW_15321	II
STMMW_15331	II
STMMW_15341	II
STMMW_15351	II
STMMW_15361	II
STMMW_15371	II
STMMW_18441	II
STMMW_28291	II
STMMW_28371	II
STMMW_34021	II
STM1092	II
STMMW_12561	II
STMMW_28381	II
STMMW_28391	II
STMMW_28411	II
STMMW_37041	II
STMMW_37051	II
STMMW_12551	II
STMMW_37061	II
STMMW_37071	II
STMMW_37081	II
STMMW_42081	II/IIIa
STMMW_42091	II/IIIa
STMMW_42101	II/IIIa/IIIb

locus	subspecies
STMMW_37561	IIIa
STMMW_37641	IIIa
STMMW_37651	IIIa
STMMW_42151	IIIa
STMMW_43841	IIIa
STMMW_43861	IIIa
STMMW_43881	IIIa
STMMW_43891	IIIa
STMMW_43901	IIIa
STMMW_43921	IIIa
STMMW_44141	IIIa
STMMW_44541	IIIa
STMMW_44881	IIIa
STMMW_22041	IIIa
STMMW_21301	IIIa/IIIb/IV
STMMW_21311	IIIa/IIIb/IV
STMMW_21331	IIIa/IIIb/IV
STMMW_21341	IIIa/IIIb/IV
STMMW_16161	IIIa/Novel_B
STMMW_05791	IIIa/*S.bongori*
STMMW_06201	IIIa/*S.bongori*
STMMW_19431	IIIa/*S.bongori*
STMMW_24261	IIIa/*S.bongori*
STMMW_06121	IIIa/*S.bongori*/Novel_B
STMMW_06161	IIIa/*S.bongori*/Novel_B
STMMW_06171	IIIa/*S.bongori*/Novel_B
STMMW_06181	IIIa/*S.bongori*/Novel_B
STMMW_37631	IIIa/VI
STMMW_31021	IIIa/VI/*S.bongori*
STM3012	IIIa/VII
STMMW_27411	IIIb/*S.bongori*
STMMW_27421	IIIb/*S.bongori*
STMMW_27431	IIIb/*S.bongori*
STMMW_27441	IIIb/*S.bongori*
STMMW_01491	IV
STMMW_20411	IV

STMMW_42641	II/IIIa/IIIb
STMMW_42651	II/IIIa/IIIb
STMMW_44481	II/IIIa/IV/*S.bongori*
STMMW_11021	II/*Novel_B*
STMMW_28741	II/Novel_C
STMMW_28751	II/Novel_C
STMMW_13981	II/*S.bongori*
STMMW_13991	II/*S.bongori*
STMMW_14001	II/*S.bongori*
STMMW_14021	II/*S.bongori*
STMMW_14031	II/*S.bongori*
STMMW_14041	II/*S.bongori*
STMMW_14051	II/*S.bongori*
STMMW_14061	II/*S.bongori*
STMMW_14071	II/*S.bongori*
STMMW_14081	II/*S.bongori*
STMMW_14091	II/*S.bongori*
STMMW_14101	II/*S.bongori*
STMMW_14111	II/*S.bongori*
STMMW_14121	II/*S.bongori*
STMMW_14131	II/*S.bongori*
STMMW_14141	II/*S.bongori*
STMMW_14151	II/*S.bongori*
STMMW_14161	II/*S.bongori*
STMMW_14171	II/*S.bongori*
STMMW_14181	II/*S.bongori*
STMMW_14191	II/*S.bongori*
STMMW_14201	II/*S.bongori*
STMMW_14211	II/*S.bongori*
STMMW_14221	II/*S.bongori*
STMMW_14231	II/*S.bongori*
STMMW_14241	II/*S.bongori*
STMMW_14251	II/*S.bongori*
STMMW_14261	II/*S.bongori*
STMMW_21691	II/*S.bongori*/Novel_B
STMMW_11061	II/VI
STMMW_11071	II/VI
STMMW_30841	II/VI/*S.bongori*/Novel_C
STMMW_30851	II/VI/*S.bongori*/Novel_C
STMMW_30861	II/VI/*S.bongori*/Novel_C
STMMW_30871	II/VI/*S.bongori*/Novel_C
STMMW_30881	II/VI/*S.bongori*/Novel_C
STMMW_30891	II/VI/*S.bongori*/Novel_C
STMMW_00091	IIIa
STMMW_00101	IIIa
STMMW_01611	IIIa
STMMW_01221	IV
STMMW_18431	IV
STMMW_20501	IV/*S.bongori*
STMMW_04631	Novel_B
STMMW_08391	Novel_B
STMMW_08401	Novel_B
STMMW_08411	Novel_B
STMMW_08421	Novel_B
STMMW_08431	Novel_B
STMMW_24971	Novel_B
STMMW_32761	Novel_C
SPAB_04503	*S.bongori*
STM4351	*S.bongori*
STMMW_03311	*S.bongori*
STMMW_11091	*S.bongori*
STMMW_11101	*S.bongori*
STMMW_11111	*S.bongori*
STMMW_11121	*S.bongori*
STMMW_11131	*S.bongori*
STMMW_11141	*S.bongori*
STMMW_11151	*S.bongori*
STMMW_11161	*S.bongori*
STMMW_11171	*S.bongori*
STMMW_11181	*S.bongori*
STMMW_12591	*S.bongori*
STMMW_13961	*S.bongori*
STMMW_13971	*S.bongori*
STMMW_14271	*S.bongori*
STMMW_15861	*S.bongori*
STMMW_29361	*S.bongori*
STMMW_29371	*S.bongori*
STMMW_29381	*S.bongori*
STMMW_29391	*S.bongori*
STMMW_29401	*S.bongori*
STMMW_29411	*S.bongori*
STMMW_29421	*S.bongori*
STMMW_37801	*S.bongori*
STMMW_37811	*S.bongori*
STMMW_37821	*S.bongori*
STMMW_37831	*S.bongori*
STMMW_06111	*S.bongori*/Novel_B
STMMW_06131	*S.bongori*/Novel_B
STMMW_06141	*S.bongori*/Novel_B
STMMW_06151	*S.bongori*/Novel_B
STMMW_23791	*S.bongori*/Novel_C
STMMW_23801	*S.bongori*/Novel_C

STMMW_01621	IIIa
STMMW_04911	IIIa
STMMW_07481	IIIa
STMMW_07491	IIIa
STMMW_07501	IIIa
STMMW_09341	IIIa
STMMW_09351	IIIa
STMMW_09361	IIIa
STMMW_09971	IIIa
STMMW_11491	IIIa
STMMW_11501	IIIa
STMMW_12701	IIIa
STMMW_12931	IIIa
STMMW_13251	IIIa
STMMW_13741	IIIa
STMMW_14811	IIIa
STMMW_15771	IIIa
STMMW_15791	IIIa
STMMW_15801	IIIa
STMMW_16131	IIIa
STMMW_16991	IIIa
STMMW_21731	IIIa
STMMW_21741	IIIa
STMMW_21751	IIIa
STMMW_22081	IIIa
STMMW_22091	IIIa
STMMW_22181	IIIa
STMMW_22191	IIIa
STMMW_23211	IIIa
STMMW_23221	IIIa
STMMW_23231	IIIa
STMMW_25861	IIIa
STMMW_28761	IIIa
STMMW_28771	IIIa
STMMW_28791	IIIa
STMMW_31491	IIIa
STMMW_32331	IIIa
STMMW_34703	IIIa
STMMW_35301	IIIa
STMMW_35741	IIIa
STMMW_35751	IIIa
STMMW_35761	IIIa
STMMW_36521	IIIa
STMMW_37551	IIIa

STMMW_23811	*S.bongori*/Novel_C
STMMW_23821	*S.bongori*/Novel_C
STMMW_23831	*S.bongori*/Novel_C
STMMW_24731	*S.bongori*/VII
STMMW_24741	*S.bongori*/VII
STMMW_24751	*S.bongori*/VII
STMMW_24761	*S.bongori*/VII
STMMW_24771	*S.bongori*/VII
STMMW_24781	*S.bongori*/VII
STMMW_24791	*S.bongori*/VII
STMMW_24801	*S.bongori*/VII
STMMW_24821	*S.bongori*/VII
STMMW_24831	*S.bongori*/VII
STMMW_24841	*S.bongori*/VII
STMMW_24851	*S.bongori*/VII
STMMW_24861	*S.bongori*/VII
STMMW_24871	*S.bongori*/VII
STMMW_24881	*S.bongori*/VII
STMMW_24891	*S.bongori*/VII
STMMW_42281	*S.bongori*/VII
STMMW_42301	*S.bongori*/VII
STMMW_42311	*S.bongori*/VII
STMMW_12581	VI
STMMW_18001	VI
STMMW_24431	VI
STMMW_27481	VI
STMMW_27951	VI
STMMW_27961	VI
STMMW_27971	VI
STMMW_31261	VI
STMMW_36341	VI
STMMW_42771	VI
STMMW_16601	VI/Novel_B/Novel_C
STMMW_16611	VI/Novel_B/Novel_C
STMMW_33241	VI/*S.bongori*/Novel_B
STMMW_15051	VII
STMMW_16181	VII
STMMW_26851	VII
STMMW_26861	VII
STMMW_27041	VII
STMMW_27051	VII
STMMW_27061	VII
STMMW_42331	VII
STMMW_42391	VII

STRUCTURE analysis using EBcgMLSTv2.0 at 17 populations (A) and STRUCTURE analysis of genus core genome scheme at 16 populations (B). STRUCTURE plots of 73 isolates: 7 subspecies I, II, IIIa, IIIb, IV, VI, VII, novel B, novel C and *S. bongori* and 3 novel A isolates, edited using the DISTRUCT tool. These plots were created with a burn-in of 100,000, an MCMC of 200,000 and a K of 11 and compared EBcgMLSTv2.0 with SalmcgMLSTv1.0.

A: Plot showing that at a K of 17 the STRUCTURE algorithm is capable of identifying all the *S. enterica* subspecies and *S. bongori* when using EBcgMLSTv2.0. All of the subspecies and *S. bongori* were identified at a K of 17. At this value of K there was a significant level of admixture between Typhi and Paratyphi A isolates, which are typically highly distinct from the other subspecies I isolates, and the rest of the subspecies I isolates. The subspecies I serovar Oranienburg isolate was also very admixed with several different populations represented within the single population

B: Plot showing that at a K of 16 the STRUCTURE algorithm identified a very similar population structure using the SalmcgMLSTv1.0 scheme as the EBcgMLSTv2.0 scheme identified at a K of 17. Once again all of the subspecies and *S bongori* are identified and there is a high level of admixture within subspecies I. The subspecies I serovars Typhi and Paratyphi A are once again identified as highly distinct populations from the rest of the subspecies I isolates and the serovar Oranienburg isolate was again very admixed.

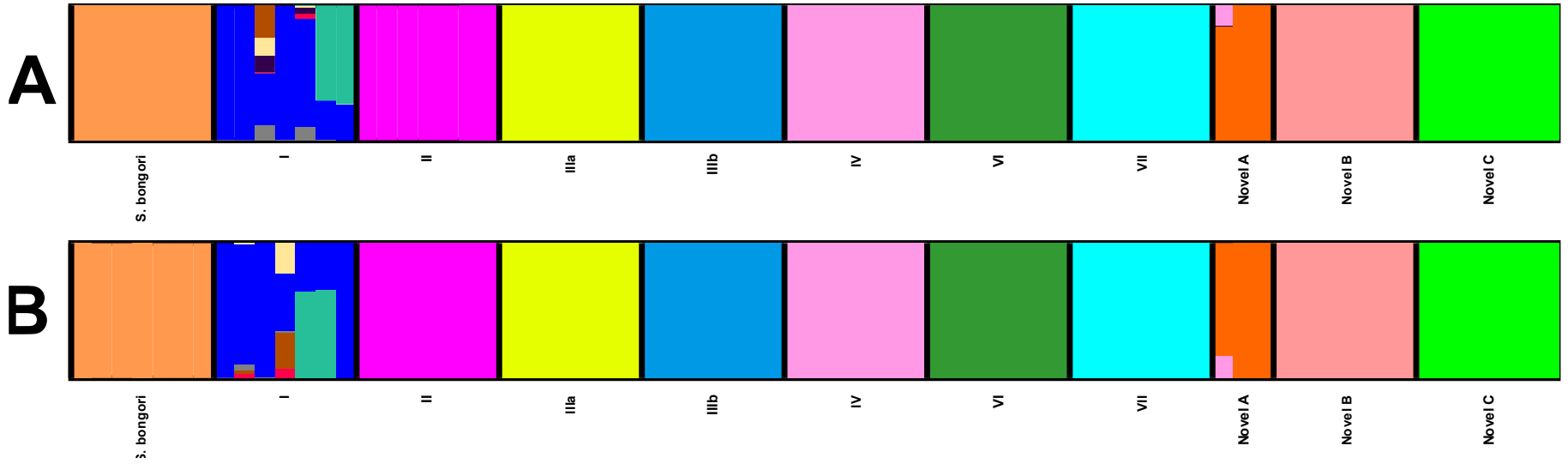


Table of all isolates within the MSTree analyses (Chapter Five)

PubmIst ID	Analysis Subspecies	Serovar (Enterobase)
16167	I	Infantis
16183	I	Montevideo
16190	I	Typhimurium
16207	I	Oranienburg
17235	I	Java
17298	I	Paratyphi A
17326	I	Typhi
12643	II	N/A
13335	II	N/A
13852	II	N/A
16006	II	N/A
16229	II	N/A
16870	II	N/A
17101	II	N/A
16169	II/XI/Novel	N/A
16057	IIIb	N/A
16063	IIIb	N/A
16329	IIIb	N/A
16456	IIIb	N/A
16466	IIIb	N/A
16597	IIIb	N/A
16717	IIIb	N/A
12651	IV	N/A
13596	IV	N/A
16085	IV	N/A
16402	IV	N/A
16413	IV	N/A
16608	IV	N/A
16710	IV	N/A
15280	IX	N/A
15979	IX	N/A
16143	IX	N/A
16155	IX	N/A
16158	IX	N/A
16668	IX	N/A
16756	IX	N/A
11853	*S. arizonae*	N/A
15051	*S. arizonae*	N/A
16481	*S. arizonae*	N/A
16644	*S. arizonae*	N/A
16751	*S. arizonae*	N/A
16803	*S. arizonae*	N/A
16941	*S. arizonae*	N/A
13269	*S.bongori*	N/A
16640	II	N/A
16426	II	N/A
16204	II	N/A
17099	II	N/A
16230	II	N/A
13586	II	N/A
16634	II	N/A
16444	II	N/A
17104	II	N/A
11798	II	N/A
16581	II	N/A
16359	II	N/A
14004	II	N/A
16824	II	N/A
16590	II	N/A
14825	II	N/A
14710	II	N/A
16026	II	N/A
16345	II	N/A
13801	II	N/A
14291	II	N/A
17070	IIIb	N/A
12934	IIIb	N/A
17033	IIIb	N/A
15960	IIIb	N/A
16665	IIIb	N/A
13065	IIIb	N/A
17152	IIIb	N/A
16537	IIIb	N/A
13235	IIIb	N/A
12932	IIIb	N/A
12455	IIIb	N/A
11694	IIIb	N/A
17019	IIIb	N/A
16431	IIIb	N/A
15341	IIIb	N/A
16931	IIIb	N/A
17076	IIIb	N/A
16417	IIIb	N/A
16952	IIIb	N/A
16420	IIIb	N/A
14787	IIIb	N/A
17081	IIIb	N/A
14518	IIIb	N/A

16100	*S.bongori*	N/A
16206	*S.bongori*	N/A
16221	*S.bongori*	N/A
16267	*S.bongori*	N/A
16392	*S.bongori*	N/A
16570	*S.bongori*	N/A
12601	VI	N/A
12603	VI	N/A
12605	VI	N/A
12645	VI	N/A
12848	VI	N/A
14055	VI	N/A
16964	VI	N/A
13892	VII	N/A
16163	VII	N/A
16164	VII	N/A
17179	VII	N/A
17184	VII	N/A
16111	VIII	N/A
16141	VIII	N/A
16142	VIII	N/A
9629	X	N/A
12469	X	N/A
15989	X	N/A
16145	X	N/A
16159	X	N/A
16521	X	N/A
16686	X	N/A
12480	XI	N/A
16147	XI	N/A
16148	XI	N/A
12664	VII	N/A
16552	VII	N/A
16278	I	Hadar
16208	I	Agona
17303	I	Saintpaul
16282	I	Mbandaka
17199	I	Bareilly
17226	I	Hadar
17256	I	Montevideo
16192	I	Montevideo
16212	I	Typhimurium
16257	I	Hadar
17372	I	Virchow
17373	I	Virchow
16385	I	Bareilly
16254	I	Montevideo
16379	I	Saintpaul
17232	I	Infantis
16188	I	Newport
17364	I	Virchow
17275	I	Newport
16209	I	Newport

16289	IIIb	N/A
16967	IIIb	N/A
14830	IIIb	N/A
16075	IIIb	N/A
16783	IIIb	N/A
16421	IIIb	N/A
16778	IIIb	N/A
16804	IIIb	N/A
16565	IIIb	N/A
17107	IIIb	N/A
16939	IIIb	N/A
12048	IIIb	N/A
16627	IIIb	N/A
16071	IIIb	N/A
16832	IIIb	N/A
17077	IIIb	N/A
16925	IIIb	N/A
16314	IIIb	N/A
17030	IIIb	N/A
16930	IIIb	N/A
16332	IIIb	N/A
13236	IIIb	N/A
16650	IIIb	N/A
16042	IIIb	N/A
16086	IIIb	N/A
17111	IIIb	N/A
13521	IIIb	N/A
16248	IIIb	N/A
16233	IIIb	N/A
17052	IIIb	N/A
16835	IIIb	N/A
16550	IIIb	N/A
16944	IIIb	N/A
14511	IIIb	N/A
16404	IIIb	N/A
16828	IIIb	N/A
16866	IIIb	N/A
16563	IIIb	N/A
16496	IIIb	N/A
12854	IIIb	N/A
16445	IIIb	N/A
16782	IIIb	N/A
13991	IIIb	N/A
16943	IIIb	N/A
16902	IIIb	N/A
16138	IIIb	N/A
17154	IIIb	N/A
14529	IIIb	N/A
16037	IIIb	N/A
12069	IIIb	N/A
16544	IIIb	N/A
16755	IIIb	N/A
17072	IIIb	N/A

16382	I	Kentucky	13482	IIIb	N/A
16272	I	Java	16250	IIIb	N/A
17258	I	Montevideo	16505	IIIb	N/A
16378	I	Kentucky	16246	IIIb	N/A
16275	I	Montevideo	15288	IIIb	N/A
17321	I	Newport	14483	IIIb	N/A
17305	I	Saintpaul	16477	IIIb	N/A
16213	I	Oranienburg	11745	IIIb	N/A
16200	I	Virchow	12842	IIIb	N/A
16384	I	Bareilly	16805	IIIb	N/A
16181	I	Stanley	16475	IIIb	N/A
17294	I	Oranienburg	14123	IIIb	N/A
17281	I	Newport	16890	IIIb	N/A
17192	I	Agona	16429	IIIb	N/A
16195	I	Newport	17132	IIIb	N/A
17227	I	Hadar	16236	IIIb	N/A
16259	I	Enteritidis	17056	IIIb	N/A
16280	I	Agona	16784	IIIb	N/A
16377	I	Saintpaul	16008	IIIb	N/A
16203	I	Montevideo	16604	IIIb	N/A
17253	I	Mbandaka	16029	IIIb	N/A
17288	I	Oranienburg	16837	IIIb	N/A
16372	I	Saintpaul	16735	IIIb	N/A
16380	I	Senftenberg	15973	IIIb	N/A
16260	I	Newport	11933	IIIb	N/A
16182	I	Paratyphi A	16245	IIIb	N/A
16288	I	Newport	16986	IIIb	N/A
17330	I	Senftenberg	16704	IIIb	N/A
17241	I	Kentucky	16732	IIIb	N/A
17225	I	Hadar	16631	IIIb	N/A
17369	I	Virchow	16016	IIIb	N/A
17317	I	Java	13422	IIIb	N/A
16376	I	Kentucky	16483	IIIb	N/A
16210	I	Oranienburg	14005	IIIb	N/A
16191	I	Typhimurium	16321	IIIb	N/A
17233	I	Java	17009	IIIb	N/A
16171	I	Typhimurium	16303	IIIb	N/A
16177	I	Stanley	16494	IIIb	N/A
16074	I	Oranienburg	16044	IIIb	N/A
16175	I	Oranienburg	16495	IIIb	N/A
17259	I	Montevideo	16137	IIIb	N/A
17203	I	Bareilly	16862	IIIb	N/A
17287	I	Oranienburg	16899	IIIb	N/A
17216	I	Braenderup	16793	IIIb	N/A
17274	I	Newport	16754	IIIb	N/A
16201	I	Virchow	12207	IIIb	N/A
16283	I	Mbandaka	16318	IIIb	N/A
16255	I	Thompson	16722	IIIb	N/A
16211	I	Typhimurium	16010	IIIb	N/A
16185	I	Enteritidis	16253	IIIb	N/A
16256	I	Newport	15962	IIIb	N/A
16387	I	Senftenberg	17068	IIIb	N/A
16388	I	Saintpaul	13593	IIIb	N/A

16196	I	Virchow
17352	I	Thompson
17222	I	Enteritidis
16386	I	Senftenberg
17345	I	Stanley
17264	I	Montevideo
17230	I	Infantis
16270	I	Java
16285	I	Typhi
16186	I	Enteritidis
16066	I	Newport
16070	I	Java
16258	I	Virchow
16284	I	Paratyphi A
17359	I	Typhimurium
17102	II	N/A
16507	II	N/A
14194	II	N/A
15986	II	N/A
14411	II	N/A
16001	II	N/A
16424	II	N/A
11943	II	N/A
15987	II	N/A
16678	II	N/A
11684	II	N/A
16339	II	N/A
12835	II	N/A
16564	II	N/A
16205	II	N/A
16764	II	N/A
16133	II	N/A
16027	II	N/A
14006	II	N/A
12195	II	N/A
16091	II	N/A
15988	II	N/A
13256	II	N/A
16000	II	N/A
15984	II	N/A
16028	II	N/A
15983	II	N/A
13819	II	N/A
12632	II	N/A
15991	II	N/A
16243	II	N/A
16651	II	N/A
16007	II	N/A
15994	II	N/A
11579	II	N/A
12649	II	N/A
16593	II	N/A
13853	II	N/A
17175	IIIb	N/A
17074	IIIb	N/A
11912	IIIb	N/A
16701	IIIb	N/A
16961	IIIb	N/A
17021	IIIb	N/A
16441	IIIb	N/A
14526	IIIb	N/A
17050	IIIb	N/A
16916	IIIb	N/A
16620	IIIb	N/A
12935	IIIb	N/A
16854	IIIb	N/A
16416	IIIb	N/A
16081	IIIb	N/A
16739	IIIb	N/A
11711	IIIb	N/A
16723	IIIb	N/A
16443	IIIb	N/A
16389	IIIb	N/A
16390	IIIb	N/A
16976	IIIb	N/A
16927	IIIb	N/A
17144	IIIb	N/A
16822	IIIb	N/A
16558	IIIb	N/A
13545	IIIb	N/A
16058	IIIb	N/A
16428	IIIb	N/A
16053	IIIb	N/A
16068	IIIb	N/A
16014	IIIb	N/A
14180	IIIb	N/A
16442	IIIb	N/A
12006	IIIb	N/A
16745	IIIb	N/A
16317	IIIb	N/A
16301	IIIb	N/A
16831	IIIb	N/A
16789	IIIb	N/A
15375	IIIb	N/A
16719	IIIb	N/A
17158	IIIb	N/A
17023	IIIb	N/A
13443	IIIb	N/A
14660	IIIb	N/A
16968	IIIb	N/A
16555	IIIb	N/A
16792	IIIb	N/A
15961	IIIb	N/A
16712	IIIb	N/A
16367	IIIb	N/A
16838	IIIb	N/A

17064	II	N/A	16819	IIIb	N/A
16612	II	N/A	17140	IIIb	N/A
16698	II	N/A	16694	IIIb	N/A
13249	II	N/A	11704	IIIb	N/A
16017	II	N/A	17078	IIIb	N/A
16011	II	N/A	13260	IIIb	N/A
15990	II	N/A	16901	IIIb	N/A
17092	II	N/A	17028	IIIb	N/A
16264	II	N/A	16794	IIIb	N/A
17071	II	N/A	17062	IIIb	N/A
16009	II	N/A	12963	IIIb	N/A
12836	II	N/A	16605	IIIb	N/A
17089	II	N/A	16541	IIIb	N/A
17067	II	N/A	17156	IIIb	N/A
14371	II	N/A	16528	IIIb	N/A
17022	II	N/A	14524	IIIb	N/A
16423	II	N/A	13925	IIIb	N/A
17103	II	N/A	16320	IIIb	N/A
16348	II	N/A	16315	IIIb	N/A
16003	II	N/A	16069	IIIb	N/A
13672	II	N/A	16561	IIIb	N/A
16647	II	N/A	15965	IIIb	N/A
17174	II	N/A	13272	IIIb	N/A
16023	II	N/A	16473	IIIb	N/A
12471	II	N/A	16433	IIIb	N/A
16757	II	N/A	17054	IIIb	N/A
17098	II	N/A	17051	IIIb	N/A
14542	II	N/A	16508	IIIb	N/A
12622	II	N/A	17058	IIIb	N/A
16019	II	N/A	16024	IIIb	N/A
17069	II	N/A	16874	IIIb	N/A
15981	II	N/A	17157	IIIb	N/A
16553	II	N/A	13273	IIIb	N/A
14333	II	N/A	16276	IIIb	N/A
17080	II	N/A	17134	IIIb	N/A
16514	II	N/A	16526	IIIb	N/A
12047	II	N/A	16602	IIIb	N/A
16497	II	N/A	14521	IIIb	N/A
13308	II	N/A	12485	IIIb	N/A
13559	II	N/A	16758	IIIb	N/A
17040	II	N/A	17151	IIIb	N/A
16654	II	N/A	16884	IIIb	N/A
11637	II	N/A	15400	IIIb	N/A
16542	II	N/A	13995	IIIb	N/A
16168	II	N/A	16484	IIIb	N/A
14022	II	N/A	16286	IIIb	N/A
16683	II	N/A	17020	IIIb	N/A
16414	II	N/A	13427	IIIb	N/A
12270	II	N/A	17055	IIIb	N/A
17085	II	N/A	17149	IIIb	N/A
15993	II	N/A	12465	IIIb	N/A
16787	II	N/A	15459	IIIb	N/A
17093	II	N/A	16059	IIIb	N/A

17057	II	N/A	16244	IIIb	N/A
16366	IIIb	N/A	16753	IIIb	N/A
16082	IIIb	N/A	16938	IIIb	N/A
14137	IIIb	N/A	16036	IIIb	N/A
16045	IIIb	N/A	16061	IIIb	N/A
16532	IIIb	N/A	16516	IIIb	N/A
14921	IIIb	N/A	16727	IIIb	N/A
16300	IIIb	N/A	17039	IIIb	N/A
14782	IIIb	N/A	13544	IIIb	N/A
17059	IIIb	N/A	16705	IIIb	N/A
16845	IIIb	N/A	16851	IIIb	N/A
16910	IIIb	N/A	16891	IIIb	N/A
16073	IIIb	N/A	12885	IIIb	N/A
16786	IIIb	N/A	16596	IIIb	N/A
16861	IIIb	N/A	17173	IIIb	N/A
16327	IIIb	N/A	16543	IIIb	N/A
16729	IIIb	N/A	17027	IIIb	N/A
16826	IIIb	N/A	17017	IIIb	N/A
17170	IIIb	N/A	17165	IIIb	N/A
16818	IIIb	N/A	16325	IIIb	N/A
16214	IIIb	N/A	17166	IIIb	N/A
12250	IIIb	N/A	16025	IIIb	N/A
12933	IIIb	N/A	16947	IIIb	N/A
16801	IIIb	N/A	16882	IIIb	N/A
16425	IIIb	N/A	17003	IIIb	N/A
16373	IIIb	N/A	17043	IIIb	N/A
17018	IIIb	N/A	14508	IIIb	N/A
11783	IIIb	N/A	16998	IIIb	N/A
16296	IIIb	N/A	16724	IIIb	N/A
16234	IIIb	N/A	16860	IIIb	N/A
16304	IIIb	N/A	16076	IIIb	N/A
16292	IIIb	N/A	16893	IIIb	N/A
13543	IIIb	N/A	17160	IIIb	N/A
16583	IIIb	N/A	17155	IIIb	N/A
16661	IIIb	N/A	16562	IIIb	N/A
12397	IIIb	N/A	13252	IIIb	N/A
16328	IIIb	N/A	16556	IIIb	N/A
16022	IIIb	N/A	16848	IIIb	N/A
16584	IIIb	N/A	16297	IIIb	N/A
12454	IIIb	N/A	17007	IIIb	N/A
16802	IIIb	N/A	16625	IIIb	N/A
16060	IIIb	N/A	16912	IIIb	N/A
12715	IIIb	N/A	16601	IIIb	N/A
16652	IIIb	N/A	16933	IIIb	N/A
14121	IIIb	N/A	16534	IIIb	N/A
16050	IIIb	N/A	11517	IIIb	N/A
14179	IIIb	N/A	16653	IIIb	N/A
16293	IIIb	N/A	17047	IIIb	N/A
16603	IIIb	N/A	16908	IIIb	N/A
16232	IIIb	N/A	16799	IIIb	N/A
16459	IIIb	N/A	16983	IIIb	N/A
16797	IIIb	N/A	17066	IIIb	N/A
12028	IIIb	N/A	11643	IIIb	N/A

16279	IIIb	N/A	16450	IIIb	N/A
16834	IIIb	N/A	16648	IIIb	N/A
16324	IIIb	N/A	16566	IIIb	N/A
17146	IIIb	N/A	16633	IIIb	N/A
11766	IIIb	N/A	14824	IIIb	N/A
16294	IIIb	N/A	13585	IIIb	N/A
12027	IIIb	N/A	16811	IIIb	N/A
16307	IIIb	N/A	16482	IIIb	N/A
16440	IIIb	N/A	16589	IIIb	N/A
17060	IIIb	N/A	16551	IIIb	N/A
11733	IIIb	N/A	16107	IIIb	N/A
16628	IIIb	N/A	17011	IIIb	N/A
14530	IIIb	N/A	11873	IIIb	N/A
16511	IIIb	N/A	13102	IIIb	N/A
12486	IIIb	N/A	16600	IIIb	N/A
16790	IIIb	N/A	16432	IIIb	N/A
16305	IIIb	N/A	16077	IIIb	N/A
16054	IIIb	N/A	17034	IIIb	N/A
17075	IIIb	N/A	16741	IIIb	N/A
15117	IIIb	N/A	16680	IIIb	N/A
16302	IIIb	N/A	16586	IIIb	N/A
16906	IIIb	N/A	16333	IIIb	N/A
16911	IIIb	N/A	14510	IIIb	N/A
11765	IIIb	N/A	12840	IIIb	N/A
17037	IIIb	N/A	16951	IIIb	N/A
16018	IIIb	N/A	16306	IIIb	N/A
16464	IIIb	N/A	16559	IIIb	N/A
16046	IIIb	N/A	16844	IIIb	N/A
16725	IIIb	N/A	16447	IIIb	N/A
11973	IIIb	N/A	13286	IIIb	N/A
16035	IIIb	N/A	16934	IIIb	N/A
16515	IIIb	N/A	14520	IIIb	N/A
12843	IIIb	N/A	15964	IIIb	N/A
16726	IIIb	N/A	16728	IIIb	N/A
13856	IIIb	N/A	16363	IIIb	N/A
16051	IIIb	N/A	16823	IIIb	N/A
11631	IIIb	N/A	14919	IIIb	N/A
16849	IIIb	N/A	16877	IIIb	N/A
16731	IIIb	N/A	16643	IIIb	N/A
16030	IIIb	N/A	16043	IIIb	N/A
15348	IIIb	N/A	15292	IIIb	N/A
16055	IV	N/A	16868	IIIb	N/A
16032	IV	N/A	16617	IIIb	N/A
11990	IV	N/A	16342	IIIb	N/A
16833	IV	N/A	12222	IIIb	N/A
16738	IV	N/A	16298	IIIb	N/A
17127	IV	N/A	16235	IIIb	N/A
16761	IV	N/A	13401	IIIb	N/A
16980	IV	N/A	17061	IIIb	N/A
16718	IV	N/A	16853	IIIb	N/A
16842	IV	N/A	16311	IIIb	N/A
13403	IV	N/A	16896	IIIb	N/A
12602	IV	N/A	14522	IIIb	N/A

16287	IV	N/A
16033	IV	N/A
16989	IV	N/A
12661	IV	N/A
13295	IV	N/A
16226	IV	N/A
15958	IV	N/A
16064	IV	N/A
14367	IV	N/A
16607	IV	N/A
16709	IV	N/A
16699	IV	N/A
14075	IV	N/A
16873	IV	N/A
16721	IV	N/A
16865	IV	N/A
16748	IV	N/A
12654	IV	N/A
16715	IV	N/A
16903	IV	N/A
16759	IV	N/A
16527	IV	N/A
16356	IV	N/A
13464	IV	N/A
16703	IV	N/A
16689	IV	N/A
12618	IV	N/A
16796	IV	N/A
16262	IV	N/A
13471	IV	N/A
16788	IV	N/A
14134	IV	N/A
12462	IV	N/A
16357	IV	N/A
14195	IV	N/A
16227	IV	N/A
16365	IV	N/A
12846	IV	N/A
13356	IV	N/A
16231	IV	N/A
12474	IV	N/A
15976	IV	N/A
16867	IV	N/A
13696	IV	N/A
16575	IV	N/A
12930	IV	N/A
16065	IV	N/A
16682	IV	N/A
13371	IV	N/A
16747	IV	N/A
16685	IV	N/A
12954	IV	N/A
14131	IV	N/A
13476	IIIb	N/A
12408	IV	N/A
17031	IV	N/A
16218	IV	N/A
16290	IV	N/A
17164	IV	N/A
16852	IV	N/A
16462	IV	N/A
17002	IV	N/A
16491	IV	N/A
14428	IV	N/A
12749	IV	N/A
16872	IV	N/A
13304	IV	N/A
16626	IV	N/A
16048	IV	N/A
13418	IV	N/A
16969	IV	N/A
16914	IV	N/A
13887	IV	N/A
16322	IV	N/A
12659	IV	N/A
17012	IV	N/A
12510	IV	N/A
16498	IV	N/A
12971	IV	N/A
17150	IV	N/A
16946	IV	N/A
16973	IV	N/A
17136	IV	N/A
12742	IV	N/A
13462	IV	N/A
12662	IV	N/A
16436	IV	N/A
17008	IV	N/A
16571	IV	N/A
14359	IV	N/A
16795	IV	N/A
13410	IV	N/A
16829	IV	N/A
16895	IV	N/A
16606	IV	N/A
16781	IV	N/A
17041	IV	N/A
16932	IV	N/A
16391	IV	N/A
12728	IV	N/A
712	IV	N/A
17168	IV	N/A
11989	IV	N/A
16996	IV	N/A
16140	IV	N/A
13608	IV	N/A

16716	IV	N/A
16649	IV	N/A
16836	IV	N/A
14017	IV	N/A
16713	IV	N/A
15977	IV	N/A
16576	IV	N/A
16034	IV	N/A
16360	IV	N/A
13412	IV	N/A
16646	IV	N/A
15959	IV	N/A
16485	IV	N/A
16692	IV	N/A
13449	IV	N/A
14444	IV	N/A
16775	IV	N/A
16785	IV	N/A
13369	IV	N/A
16875	IV	N/A
12736	IV	N/A
14419	IV	N/A
13461	IV	N/A
16419	IV	N/A
16312	IV	N/A
16310	IV	N/A
16706	IV	N/A
14378	IV	N/A
17095	IX	N/A
16815	*S. arizonae*	N/A
15377	*S. arizonae*	N/A
17139	*S. arizonae*	N/A
13863	*S. arizonae*	N/A
13607	*S. arizonae*	N/A
14926	*S. arizonae*	N/A
13665	*S. arizonae*	N/A
11635	*S. arizonae*	N/A
16744	*S. arizonae*	N/A
16840	*S. arizonae*	N/A
16695	*S. arizonae*	N/A
16806	*S. arizonae*	N/A
16632	*S. arizonae*	N/A
16610	*S. arizonae*	N/A
13914	*S. arizonae*	N/A
16098	*S. arizonae*	N/A
15975	*S. arizonae*	N/A
16592	*S. arizonae*	N/A
16281	*S. arizonae*	N/A
16299	*S. arizonae*	N/A
16165	*S. arizonae*	N/A
16512	*S. arizonae*	N/A
16779	*S. arizonae*	N/A
16830	*S. arizonae*	N/A
16313	IV	N/A
16918	IV	N/A
14167	IV	N/A
15968	IV	N/A
12482	IV	N/A
12473	IV	N/A
16094	IV	N/A
14927	IV	N/A
16038	IV	N/A
16216	IV	N/A
14097	IV	N/A
16888	IV	N/A
16997	IV	N/A
12404	IV	N/A
14354	IV	N/A
16461	IV	N/A
12525	IV	N/A
16613	IV	N/A
13669	IV	N/A
16637	IV	N/A
16642	IV	N/A
16295	IV	N/A
17128	IV	N/A
12529	IV	N/A
11796	IV	N/A
16656	IV	N/A
16687	IV	N/A
16479	IV	N/A
16319	IV	N/A
14174	IV	N/A
16937	IV	N/A
16736	IV	N/A
16434	IV	N/A
12696	IV	N/A
14311	IV	N/A
13358	IV	N/A
12606	IV	N/A
14317	IV	N/A
16962	IV	N/A
16539	IV	N/A
16737	IV	N/A
16487	IV	N/A
14157	IV	N/A
16638	IV	N/A
16624	IV	N/A
14373	IV	N/A
16355	IV	N/A
16437	IV	N/A
17153	IV	N/A
16863	IV	N/A
14476	IV	N/A
16522	IV	N/A
17045	IV	N/A

16273	*S. arizonae*	N/A
16880	*S. arizonae*	N/A
16580	*S. arizonae*	N/A
16506	*S. arizonae*	N/A
13961	*S. arizonae*	N/A
16078	*S. arizonae*	N/A
16700	*S. arizonae*	N/A
16217	*S. arizonae*	N/A
16889	*S. arizonae*	N/A
16798	*S. arizonae*	N/A
12325	*S. arizonae*	N/A
14122	*S. arizonae*	N/A
16031	*S. arizonae*	N/A
16237	*S. arizonae*	N/A
16518	*S. arizonae*	N/A
16517	*S. arizonae*	N/A
16752	*S. arizonae*	N/A
12837	*S. arizonae*	N/A
13630	*S. arizonae*	N/A
16676	*S. arizonae*	N/A
16655	*S. arizonae*	N/A
16708	*S. arizonae*	N/A
16847	*S. arizonae*	N/A
16672	*S. arizonae*	N/A
16839	*S. arizonae*	N/A
16690	*S. arizonae*	N/A
15039	*S. arizonae*	N/A
16763	*S. arizonae*	N/A
16513	*S. arizonae*	N/A
12535	*S. arizonae*	N/A
16871	*S. arizonae*	N/A
13972	*S. arizonae*	N/A
15118	*S. arizonae*	N/A
16609	*S. arizonae*	N/A
16733	*S. arizonae*	N/A
17025	*S. arizonae*	N/A
16249	*S. arizonae*	N/A
16582	*S. arizonae*	N/A
16714	*S. arizonae*	N/A
13460	*S. arizonae*	N/A
16595	*S. arizonae*	N/A
16409	*S. arizonae*	N/A
16773	*S. arizonae*	N/A
16675	*S. arizonae*	N/A
16615	*S. arizonae*	N/A
16291	*S. arizonae*	N/A
16894	*S. arizonae*	N/A
12886	*S. arizonae*	N/A
17171	*S. arizonae*	N/A
15999	*S. arizonae*	N/A
16825	*S. arizonae*	N/A
16411	*S. arizonae*	N/A
12623	*S. arizonae*	N/A

16354	IV	N/A
16950	IV	N/A
13472	IV	N/A
16639	IV	N/A
16981	IV	N/A
12395	IV	N/A
12746	IV	N/A
12484	IV	N/A
16067	IV	N/A
16816	IV	N/A
16263	IV	N/A
16523	IV	N/A
15978	IV	N/A
12422	IV	N/A
13382	IV	N/A
12423	IV	N/A
16139	IV	N/A
15974	IV	N/A
12927	IV	N/A
16900	IV	N/A
14451	IV	N/A
16897	IV	N/A
16468	IV	N/A
17048	IV	N/A
16800	IV	N/A
16864	IV	N/A
16308	IV	N/A
14497	IV	N/A
16585	IV	N/A
17005	IV	N/A
16909	IV	N/A
16881	IV	N/A
16919	IV	N/A
12845	IV	N/A
16438	IV	N/A
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16427	IV	N/A
16772	IV	N/A
16948	IV	N/A
14592	IV	N/A
16052	IV	N/A
16673	IV	N/A
16949	IV	N/A
16641	IV	N/A
16173	IV	N/A
16920	IV	N/A
14112	IV	N/A
13668	IV	N/A
16970	IV	N/A
16099	IV	N/A

16533	*S. arizonae*	N/A
16557	*S. arizonae*	N/A
16760	*S. arizonae*	N/A
15018	*S. arizonae*	N/A
12855	*S. arizonae*	N/A
16776	*S. arizonae*	N/A
16887	*S. arizonae*	N/A
16106	*S. arizonae*	N/A
16574	*S. arizonae*	N/A
13446	*S. arizonae*	N/A
16401	*S. arizonae*	N/A
13965	*S. arizonae*	N/A
16856	*S. arizonae*	N/A
16039	*S. arizonae*	N/A
16616	*S. arizonae*	N/A
16693	*S. arizonae*	N/A
16771	*S.bongori*	N/A
16269	*S.bongori*	N/A
16449	*S.bongori*	N/A
15140	*S.bongori*	N/A
16549	*S.bongori*	N/A
14904	*S.bongori*	N/A
16587	*S.bongori*	N/A
16222	*S.bongori*	N/A
13799	*S.bongori*	N/A
16274	*S.bongori*	N/A
16223	*S.bongori*	N/A
16265	*S.bongori*	N/A
12887	*S.bongori*	N/A
12049	*S.bongori*	N/A
16569	*S.bongori*	N/A
13189	*S.bongori*	N/A
16109	*S.bongori*	N/A
17142	*S.bongori*	N/A
16812	*S.bongori*	N/A
17138	*S.bongori*	N/A
15971	*S.bongori*	N/A
15972	*S.bongori*	N/A
12496	VI	N/A
12479	VI	N/A
16767	VI	N/A
16827	VI	N/A
16152	VI	N/A
13620	VI	N/A
14197	VI	N/A
16578	VI	N/A
16220	VI	N/A
15967	X	N/A
12478	X	N/A
16080	X	N/A
16102	I	Newport
17197	I	Bareilly
17329	I	Typhimurium
16465	IV	N/A
15966	IV	N/A
12724	IV	N/A
12611	IV	N/A
16062	IV	N/A
14923	IV	N/A
16993	IV	N/A
16892	IV	N/A
12505	IV	N/A
16546	IV	N/A
14417	IV	N/A
14372	IV	N/A
11976	IV	N/A
17082	IV	N/A
14026	IV	N/A
15970	IV	N/A
16040	IV	N/A
16707	IV	N/A
16439	IV	N/A
16049	IV	N/A
16538	IV	N/A
16635	IV	N/A
17145	IV	N/A
13523	IV	N/A
12495	IV	N/A
14809	IV	N/A
16923	IV	N/A
14070	IV	N/A
16056	IV	N/A
17014	IV	N/A
16430	IV	N/A
16474	IV	N/A
12494	IV	N/A
16266	IV	N/A
17126	IV	N/A
12701	IV	N/A
16992	IV	N/A
16520	IV	N/A
16991	IV	N/A
14044	IV	N/A
16982	IV	N/A
17119	IV	N/A
16554	IV	N/A
16524	IV	N/A
12521	IV	N/A
16928	IV	N/A
12668	IV	N/A
12647	IV	N/A
17001	IV	N/A
16323	IV	N/A
16471	IV	N/A
16261	IV	N/A
16734	IV	N/A

17248	I	Kentucky
17215	I	Braenderup
17201	I	Bareilly
17254	I	Montevideo
16180	I	Oranienburg
17360	I	Typhimurium
17302	I	Saintpaul
17313	I	Infantis
17266	I	Montevideo
16199	I	Thompson
17306	I	Agona
17315	I	Infantis
17217	I	Braenderup
16383	I	Saintpaul
17301	I	Java
17362	I	Virchow
16184	I	Hadar
17255	I	Montevideo
17347	I	Thompson
17261	I	Montevideo
17204	I	Bareilly
16197	I	Virchow
16189	I	Virchow
17243	I	Kentucky
17195	I	Agona
17327	I	Typhi
17282	I	Newport
17363	I	Virchow
17245	I	Kentucky
16170	I	Stanley
17280	I	Newport
16375	I	Bareilly
17320	I	Newport
17340	I	Stanley
17257	I	Montevideo
16187	I	Java
17244	I	Kentucky
17224	I	Enteritidis
17250	I	Mbandaka
16130	I	Paratyphi A
17220	I	Braenderup
17299	I	Paratyphi A
17219	I	Braenderup
16381	I	Saintpaul
17353	I	Thompson
16178	I	Montevideo
17293	I	Oranienburg
17277	I	Newport
17236	I	Java
17278	I	Newport
17361	I	Typhimurium
17214	I	Braenderup
16193	I	Mbandaka

12745	IV	N/A
16645	IV	N/A
13397	IV	N/A
14361	IV	N/A
16879	IV	N/A
16855	IV	N/A
16662	IV	N/A
17163	IV	N/A
17161	IV	N/A
13522	IV	N/A
16047	IV	N/A
12434	IV	N/A
12740	IV	N/A
12468	IV	N/A
12667	IV	N/A
16697	IX	N/A
16659	IX	N/A
17115	IX	N/A
17117	IX	N/A
16658	IX	N/A
17188	IX	N/A
13568	IX	N/A
17121	IX	N/A
16667	IX	N/A
16664	IX	N/A
16791	IX	N/A
17187	IX	N/A
17120	IX	N/A
16730	IX	N/A
16679	IX	N/A
17024	IX	N/A
16677	IX	N/A
13316	IX	N/A
16671	IX	N/A
16660	IX	N/A
17116	IX	N/A
16720	IX	N/A
16688	IX	N/A
16154	IX	N/A
16157	IX	N/A
16858	IX	N/A
16749	IX	N/A
17114	IX	N/A
17118	IX	N/A
16670	IX	N/A
16666	IX	N/A
16156	IX	N/A
16153	IX	N/A
16674	IX	N/A
16663	IX	N/A
16808	IX	N/A
16696	IX	N/A
16859	IX	N/A

17202	I	Bareilly	16669	IX	N/A
17239	I	Kentucky	15996	IX	N/A
17271	I	Newport	17094	*S. arizonae*	N/A
16371	I	Bareilly	16588	*S. arizonae*	N/A
17337	I	Senftenberg	12828	*S. arizonae*	N/A
17316	I	Infantis	12851	*S. arizonae*	N/A
17205	I	Bareilly	13904	*S. arizonae*	N/A
17194	I	Agona	16594	*S. arizonae*	N/A
17251	I	Mbandaka	17015	*S. arizonae*	N/A
17371	I	Virchow	16101	*S. arizonae*	N/A
17265	I	Montevideo	12648	*S. arizonae*	N/A
17308	I	Agona	16936	*S. arizonae*	N/A
17346	I	Stanley	16821	*S. arizonae*	N/A
17350	I	Thompson	16878	*S. arizonae*	N/A
17218	I	Braenderup	16547	*S. arizonae*	N/A
17341	I	Stanley	16809	*S. arizonae*	N/A
17193	I	Agona	16396	*S. arizonae*	N/A
17262	I	Montevideo	17035	*S. arizonae*	N/A
17269	I	Newport	15392	*S. arizonae*	N/A
17221	I	Braenderup	16488	*S. arizonae*	N/A
17365	I	Virchow	16817	*S. arizonae*	N/A
17325	I	Thompson	16959	*S. arizonae*	N/A
17307	I	Agona	16945	*S. arizonae*	N/A
17292	I	Oranienburg	17063	*S. arizonae*	N/A
17279	I	Newport	15353	*S. arizonae*	N/A
17349	I	Thompson	16621	*S. arizonae*	N/A
17200	I	Bareilly	15359	*S. arizonae*	N/A
17246	I	Kentucky	13915	*S. arizonae*	N/A
17229	I	Hadar	15388	*S. arizonae*	N/A
17368	I	Virchow	16963	*S. arizonae*	N/A
17357	I	Typhi	16529	*S. arizonae*	N/A
17331	I	Senftenberg	16955	*S. arizonae*	N/A
17247	I	Kentucky	15376	*S. arizonae*	N/A
17238	I	Kentucky	16942	*S. arizonae*	N/A
17196	I	Agona	17036	*S. arizonae*	N/A
17348	I	Thompson	12853	*S. arizonae*	N/A
17370	I	Virchow	16977	*S. arizonae*	N/A
17366	I	Virchow	16395	*S. arizonae*	N/A
17351	I	Thompson	13232	*S. arizonae*	N/A
16277	I	Newport	16994	*S. arizonae*	N/A
17228	I	Hadar	16978	*S. arizonae*	N/A
17355	I	Typhi	16460	*S. arizonae*	N/A
17335	I	Senftenberg	15396	*S. arizonae*	N/A
17291	I	Oranienburg	16711	*S. arizonae*	N/A
17295	I	Oranienburg	16984	*S. arizonae*	N/A
17249	I	Mbandaka	17016	*S. arizonae*	N/A
17314	I	Infantis	12817	*S. arizonae*	N/A
17212	I	Bareilly	16750	*S. arizonae*	N/A
17198	I	Bareilly	15360	*S. arizonae*	N/A
16179	I	Hadar	17169	*S. arizonae*	N/A
17267	I	Newport	16958	*S. arizonae*	N/A
17297	I	Paratyphi A	16079	*S. arizonae*	N/A
16198	I	Montevideo	16435	*S. arizonae*	N/A

17332	I	Senftenberg	16917	*S. arizonae*	N/A
16271	I	Newport	16850	*S. arizonae*	N/A
17285	I	Oranienburg	16820	*S. arizonae*	N/A
16202	I	Typhi	12852	*S. arizonae*	N/A
17300	I	Paratyphi A	15347	*S. arizonae*	N/A
17276	I	Newport	13903	*S. arizonae*	N/A
17342	I	Stanley	14905	*S. arizonae*	N/A
17374	I	Virchow	16540	*S. arizonae*	N/A
17206	I	Bareilly	13595	*S. arizonae*	N/A
17284	I	Newport	16422	*S. arizonae*	N/A
17286	I	Oranienburg	16536	*S. arizonae*	N/A
17367	I	Virchow	16957	*S. arizonae*	N/A
17339	I	Senftenberg	16361	*S. arizonae*	N/A
17358	I	Typhi	17004	*S. arizonae*	N/A
16103	I	Infantis	14474	*S. arizonae*	N/A
17311	I	Enteritidis	11601	*S. arizonae*	N/A
17324	I	SaintN/APaul	17046	*S. arizonae*	N/A
17231	I	Infantis	16398	*S. arizonae*	N/A
17272	I	Newport	16519	*S. arizonae*	N/A
16194	I	Paratyphi A	16921	*S. arizonae*	N/A
17208	I	Bareilly	15387	*S. arizonae*	N/A
17207	I	Bareilly	16966	*S. arizonae*	N/A
17338	I	Senftenberg	16560	*S. arizonae*	N/A
17318	I	Mbandaka	16458	*S. arizonae*	N/A
17223	I	Enteritidis	15386	*S. arizonae*	N/A
17296	I	Oranienburg	17010	*S. arizonae*	N/A
16172	I	Enteritidis	16630	*S. arizonae*	N/A
17268	I	Newport	15385	*S. arizonae*	N/A
16176	I	Virchow	13162	*S. arizonae*	N/A
17343	I	Stanley	16418	*S. arizonae*	N/A
17210	I	Bareilly	16965	*S. arizonae*	N/A
17209	I	Bareilly	17000	*S. arizonae*	N/A
17333	I	Senftenberg	16657	*S. arizonae*	N/A
17309	I	Enteritidis	16097	*S. arizonae*	N/A
17273	I	Newport	14902	*S. arizonae*	N/A
17242	I	Kentucky	15151	*S. arizonae*	N/A
17328	I	Typhi	17026	*S. arizonae*	N/A
17319	I	Mbandaka	12850	*S. arizonae*	N/A
16132	I	Typhimurium	16898	*S. arizonae*	N/A
16174	I	Oranienburg	13171	*S. arizonae*	N/A
16215	I	Braenderup	16975	*S. arizonae*	N/A
17260	I	Montevideo	15374	*S. arizonae*	N/A
16309	I	Infantis	16768	*S. arizonae*	N/A
17310	I	Enteritidis	16619	*S. arizonae*	N/A
17304	I	Saintpaul	16480	*S. arizonae*	N/A
17263	I	Montevideo	16247	*S. arizonae*	N/A
17211	I	Bareilly	14380	*S. arizonae*	N/A
17334	I	Senftenberg	16972	*S. arizonae*	N/A
16370	I	Kentucky	13268	*S. arizonae*	N/A
17270	I	Newport	13918	*S. arizonae*	N/A
17354	I	Typhi	15146	*S. arizonae*	N/A
17312	I	Hadar	16953	*S. arizonae*	N/A
17356	I	Typhi	12838	*S. arizonae*	N/A

17323	I	Paratyphi A	16135	*S. arizonae*	N/A
17252	I	Mbandaka	17167	*S. arizonae*	N/A
17240	I	Kentucky	17042	*S. arizonae*	N/A
17336	I	Senftenberg	13913	*S. arizonae*	N/A
17344	I	Stanley	17006	*S. arizonae*	N/A
16374	I	Senftenberg	16913	*S. arizonae*	N/A
17322	I	Paratyphi A	17148	*S. arizonae*	N/A
17283	I	Newport	16598	*S. arizonae*	N/A
17237	I	Kentucky	17038	*S. arizonae*	N/A
17289	I	Oranienburg	17029	*S. arizonae*	N/A
17213	I	Braenderup	16905	*S. arizonae*	N/A
17290	I	Oranienburg	16929	*S. arizonae*	N/A
17234	I	Java	14920	*S. arizonae*	N/A
16131	I	Oranienburg	17177	*S. arizonae*	N/A
16846	II	N/A	14906	*S. arizonae*	N/A
16509	II	N/A	16974	*S. arizonae*	N/A
16743	II	N/A	16904	*S. arizonae*	N/A
13560	II	N/A	17122	*S. arizonae*	N/A
16242	II	N/A	17159	*S. arizonae*	N/A
12833	II	N/A	16400	*S. arizonae*	N/A
16469	II	N/A	16399	*S. arizonae*	N/A
17100	II	N/A	16995	*S. arizonae*	N/A
16072	II	N/A	12839	*S. arizonae*	N/A
16405	II	N/A	16525	*S. arizonae*	N/A
17079	II	N/A	16629	*S. arizonae*	N/A
15985	II	N/A	14369	*S. arizonae*	N/A
16251	II	N/A	16740	*S. arizonae*	N/A
12631	II	N/A	16988	*S. arizonae*	N/A
16350	II	N/A	16915	*S. arizonae*	N/A
16611	II	N/A	16573	*S. arizonae*	N/A
16337	II	N/A	16451	*S. arizonae*	N/A
13413	II	N/A	12630	*S. arizonae*	N/A
17172	II	N/A	16777	*S. arizonae*	N/A
17091	II	N/A	13919	*S. arizonae*	N/A
16568	II	N/A	16935	*S. arizonae*	N/A
14002	II	N/A	16922	*S. arizonae*	N/A
15997	II	N/A	14614	*S. arizonae*	N/A
16104	II	N/A	16470	*S. arizonae*	N/A
12481	II	N/A	16403	*S. arizonae*	N/A
16531	II	N/A	16985	*S. arizonae*	N/A
16684	II	N/A	16530	*S. arizonae*	N/A
12497	II	N/A	13908	*S. arizonae*	N/A
16453	II	N/A	16455	*S. arizonae*	N/A
16015	II	N/A	16326	*S. arizonae*	N/A
16810	II	N/A	17130	*S. arizonae*	N/A
17065	II	N/A	16907	*S. arizonae*	N/A
16490	II	N/A	16924	*S. arizonae*	N/A
12704	II	N/A	16316	*S. arizonae*	N/A
16408	II	N/A	13229	*S. arizonae*	N/A
13419	II	N/A	16869	*S. arizonae*	N/A
13558	II	N/A	16999	*S. arizonae*	N/A
16344	II	N/A	15368	*S. arizonae*	N/A
17087	II	N/A	16406	*S. arizonae*	N/A

12492	II	N/A	17013	*S. arizonae*	N/A
16343	II	N/A	13907	*S. arizonae*	N/A
16769	II	N/A	15367	*S. arizonae*	N/A
16857	II	N/A	16971	*S. arizonae*	N/A
13764	II	N/A	12084	*S. arizonae*	N/A
16347	II	N/A	16166	*S. arizonae*	N/A
16618	II	N/A	16410	*S. arizonae*	N/A
16330	II	N/A	16622	*S. arizonae*	N/A
17106	II	N/A	16454	*S. arizonae*	N/A
16241	II	N/A	15395	*S. arizonae*	N/A
12119	II	N/A	13912	*S. arizonae*	N/A
17088	II	N/A	16136	*S. arizonae*	N/A
11801	II	N/A	12755	*S. arizonae*	N/A
13384	II	N/A	16535	*S. arizonae*	N/A
16770	II	N/A	13246	*S. arizonae*	N/A
17097	II	N/A	16926	*S. arizonae*	N/A
15998	II	N/A	16841	*S. arizonae*	N/A
16636	II	N/A	17044	*S. arizonae*	N/A
16349	II	N/A	13911	*S. arizonae*	N/A
12627	II	N/A	15384	*S. arizonae*	N/A
12698	II	N/A	13136	*S. arizonae*	N/A
17141	II	N/A	17113	*S. arizonae*	N/A
16746	II	N/A	16807	*S. arizonae*	N/A
17083	II	N/A	16990	*S. arizonae*	N/A
11755	II	N/A	16478	*S. arizonae*	N/A
12657	II	N/A	16492	*S. arizonae*	N/A
12640	II	N/A	15334	*S. arizonae*	N/A
16020	II	N/A	16397	*S. arizonae*	N/A
16240	II	N/A	14903	*S. arizonae*	N/A
16252	II	N/A	16987	*S. arizonae*	N/A
16394	II	N/A	16088	*S. arizonae*	N/A
16489	II	N/A	16780	*S. arizonae*	N/A
17176	II	N/A	16467	*S. arizonae*	N/A
16004	II	N/A	16681	*S. arizonae*	N/A
16486	II	N/A	16463	*S. arizonae*	N/A
15982	II	N/A	13916	*S. arizonae*	N/A
15963	II	N/A	15366	*S. arizonae*	N/A
13512	II	N/A	16691	*S. arizonae*	N/A
16510	II	N/A	16979	*S. arizonae*	N/A
16093	II	N/A	14448	*S. arizonae*	N/A
16338	II	N/A	15362	*S. arizonae*	N/A
16476	II	N/A	16960	*S. arizonae*	N/A
17143	II	N/A	13909	*S. arizonae*	N/A
14103	II	N/A	16368	*S. arizonae*	N/A
17125	II	N/A	16956	*S. arizonae*	N/A
16407	II	N/A	16452	*S. arizonae*	N/A
16545	II	N/A	16446	*S. arizonae*	N/A
16228	II	N/A	16702	*S. arizonae*	N/A
13407	II	N/A	16940	*S. arizonae*	N/A
15980	II	N/A	17049	*S. arizonae*	N/A
16012	II	N/A	16954	*S. arizonae*	N/A
16334	II	N/A	12139	*S.bongori*	N/A
16087	II	N/A	16362	*S.bongori*	N/A

12391	II	N/A
17147	II	N/A
17124	II	N/A
17109	II	N/A
17096	II	N/A
17110	II	N/A
16013	II	N/A
14584	II	N/A
13318	II	N/A
13519	II	N/A
11499	II	N/A
15995	II	N/A
16351	II	N/A
16567	II	N/A
15969	II	N/A
16412	II	N/A
11942	II	N/A
11552	II	N/A
16134	II	N/A
17123	II	N/A
13800	II	N/A
17105	II	N/A
16876	II	N/A
15992	II	N/A
16774	II	N/A
16335	II	N/A
16599	II	N/A
17090	II	N/A
16457	II	N/A
16219	II	N/A
16352	II	N/A
17131	II	N/A
16096	II	N/A
13766	II	N/A
16239	II	N/A
16813	II	N/A
14379	II	N/A
16742	II	N/A
13455	II	N/A
14062	II	N/A
16886	II	N/A
12834	II	N/A
16346	II	N/A
16336	II	N/A
16364	II	N/A
14806	II	N/A
14473	II	N/A
16238	II	N/A
16591	II	N/A
12625	II	N/A
16504	II	N/A
17053	II	N/A
16084	II	N/A
16224	*S.bongori*	N/A
16499	*S.bongori*	N/A
16814	*S.bongori*	N/A
16090	*S.bongori*	N/A
16503	*S.bongori*	N/A
16448	*S.bongori*	N/A
16572	*S.bongori*	N/A
16021	*S.bongori*	N/A
16110	*S.bongori*	N/A
16095	*S.bongori*	N/A
17135	*S.bongori*	N/A
16501	*S.bongori*	N/A
16358	*S.bongori*	N/A
16548	*S.bongori*	N/A
16353	*S.bongori*	N/A
16225	*S.bongori*	N/A
16415	*S.bongori*	N/A
16502	*S.bongori*	N/A
16762	*S.bongori*	N/A
16500	*S.bongori*	N/A
16614	*S.bongori*	N/A
16765	*S.bongori*	N/A
17086	*S.bongori*	N/A
16493	*S.bongori*	N/A
13306	*S.bongori*	N/A
16092	VI	N/A
16579	VI	N/A
12750	VI	N/A
12476	VI	N/A
12633	VI	N/A
16766	VI	N/A
16393	VI	N/A
17137	VI	N/A
11463	VI	N/A
16268	VI	N/A
16151	VI	N/A
12470	VI	N/A
17181	VII	N/A
17183	VII	N/A
15147	VII	N/A
16883	VII	N/A
17186	VII	N/A
16885	VII	N/A
16108	VII	N/A
17178	VII	N/A
17180	VII	N/A
16577	VII	N/A
17182	VII	N/A
17162	VII	N/A
12609	VII	N/A
13894	VII	N/A
17185	VII	N/A
17133	X	N/A

16005	II	N/A
17073	II	N/A
16341	II	N/A
16331	II	N/A
14351	II	N/A
15340	II	N/A
17084	II	N/A
16340	II	N/A
16843	II	N/A

17129	X	N/A
17112	X	N/A
12856	X	N/A
16161	X	N/A
16146	X	N/A
16162	X	N/A
17108	X	N/A
16160	X	N/A

Table of all datasets used for each analysis (Chapter Five)

PubMLST_ID	Analysis_Subspecies	Dataset A	Dataset B	Dataset C	Dataset D	Dataset E
16402	IV	Yes	Yes	Yes (secondary)		
16392	*S.bongori*	Yes	Yes	Yes (primary)		
16142	VIII	Yes	Yes	Yes (secondary)	Yes (secondary)	
16111	VIII	Yes	Yes	Yes (primary)		
15989	X	Yes	Yes	Yes (secondary)		
16148	XI	Yes	Yes	Yes (primary)	Yes (secondary)	Yes
16147	XI	Yes	Yes	Yes (secondary)	Yes (primary)	
16167	I	Yes	Yes			
16183	I	Yes	Yes			
16190	I	Yes	Yes			
16207	I	Yes	Yes			
17235	I	Yes	Yes			
17298	I	Yes	Yes			
17326	I	Yes	Yes			
12643	II	Yes	Yes			
13335	II	Yes	Yes			
13852	II	Yes	Yes			
16006	II	Yes	Yes			
16229	II	Yes	Yes			
16870	II	Yes	Yes			
17101	II	Yes	Yes			
16169	II/XI/Novel	Yes	Yes			
16057	IIIb	Yes	Yes			
16063	IIIb	Yes	Yes			
16329	IIIb	Yes	Yes			
16456	IIIb	Yes	Yes			
16466	IIIb	Yes	Yes			
16597	IIIb	Yes	Yes			
16717	IIIb	Yes	Yes			
12651	IV	Yes	Yes			
13596	IV	Yes	Yes			
16085	IV	Yes	Yes			
16413	IV	Yes	Yes			
16608	IV	Yes	Yes			
16710	IV	Yes	Yes			
16143	IX	Yes	Yes		Yes (primary)	
15280	IX	Yes	Yes			
15979	IX	Yes	Yes			

16155	IX	Yes	Yes				
16158	IX	Yes	Yes				
16668	IX	Yes	Yes				
16756	IX	Yes	Yes				
11853	*S. arizonae*	Yes	Yes				
15051	*S. arizonae*	Yes	Yes				
16481	*S. arizonae*	Yes	Yes				
16644	*S. arizonae*	Yes	Yes				
16751	*S. arizonae*	Yes	Yes				
16803	*S. arizonae*	Yes	Yes				
16941	*S. arizonae*	Yes	Yes				
13269	*S.bongori*	Yes	Yes				
16100	*S.bongori*	Yes	Yes				
16206	*S.bongori*	Yes	Yes				
16221	*S.bongori*	Yes	Yes				
16267	*S.bongori*	Yes	Yes				
16570	*S.bongori*	Yes	Yes				
16964	VI	Yes	Yes				Yes
12601	VI	Yes	Yes				
12603	VI	Yes	Yes				
12605	VI	Yes	Yes				
12645	VI	Yes	Yes				
12848	VI	Yes	Yes				
14055	VI	Yes	Yes				
13892	VII	Yes	Yes				
16163	VII	Yes	Yes				
16164	VII	Yes	Yes				
17179	VII	Yes	Yes				
17184	VII	Yes	Yes				
16141	VIII	Yes	Yes		Yes (primary)		
16145	X	Yes	Yes		Yes (primary)		
9629	X	Yes	Yes				Yes
12469	X	Yes	Yes				
16159	X	Yes	Yes				
16521	X	Yes	Yes				
16686	X	Yes	Yes				
12480	XI	Yes	Yes				
16373	IIIb	Yes		Yes (secondary)			
16278	I	Yes					
16208	I	Yes					
17303	I	Yes					
16282	I	Yes					
17199	I	Yes					
17226	I	Yes					
17256	I	Yes					
16192	I	Yes					
16212	I	Yes					

16257	I	Yes
17372	I	Yes
17373	I	Yes
16385	I	Yes
16254	I	Yes
16379	I	Yes
17232	I	Yes
16188	I	Yes
17364	I	Yes
17275	I	Yes
16209	I	Yes
16382	I	Yes
16272	I	Yes
17258	I	Yes
16378	I	Yes
16275	I	Yes
17321	I	Yes
17305	I	Yes
16213	I	Yes
16200	I	Yes
16384	I	Yes
16181	I	Yes
17294	I	Yes
17281	I	Yes
17192	I	Yes
16195	I	Yes
17227	I	Yes
16259	I	Yes
16280	I	Yes
16377	I	Yes
16203	I	Yes
17253	I	Yes
17288	I	Yes
16372	I	Yes
16380	I	Yes
16260	I	Yes
16182	I	Yes
16288	I	Yes
17330	I	Yes
17241	I	Yes
17225	I	Yes
17369	I	Yes
17317	I	Yes
16376	I	Yes
16210	I	Yes
16191	I	Yes
17233	I	Yes
16171	I	Yes

16177	I	Yes	
16074	I	Yes	
16175	I	Yes	
17259	I	Yes	
17203	I	Yes	
17287	I	Yes	
17216	I	Yes	
17274	I	Yes	
16201	I	Yes	
16283	I	Yes	
16255	I	Yes	
16211	I	Yes	
16185	I	Yes	
16256	I	Yes	
16387	I	Yes	
16388	I	Yes	
16196	I	Yes	
17352	I	Yes	
17222	I	Yes	
16386	I	Yes	
17345	I	Yes	
17264	I	Yes	
17230	I	Yes	
16270	I	Yes	
16285	I	Yes	
16186	I	Yes	
16066	I	Yes	
16070	I	Yes	
16258	I	Yes	
16284	I	Yes	
17359	I	Yes	
16133	II	Yes	Yes (primary)
17102	II	Yes	
16507	II	Yes	
14194	II	Yes	
15986	II	Yes	
14411	II	Yes	
16001	II	Yes	
16424	II	Yes	
11943	II	Yes	
15987	II	Yes	
16678	II	Yes	
11684	II	Yes	
16339	II	Yes	
12835	II	Yes	
16564	II	Yes	
16205	II	Yes	
16764	II	Yes	

16027	II	Yes
14006	II	Yes
12195	II	Yes
16091	II	Yes
15988	II	Yes
13256	II	Yes
16000	II	Yes
15984	II	Yes
16028	II	Yes
15983	II	Yes
13819	II	Yes
12632	II	Yes
15991	II	Yes
16243	II	Yes
16651	II	Yes
16007	II	Yes
15994	II	Yes
11579	II	Yes
12649	II	Yes
16593	II	Yes
13853	II	Yes
17064	II	Yes
16612	II	Yes
16698	II	Yes
13249	II	Yes
16017	II	Yes
16011	II	Yes
15990	II	Yes
17092	II	Yes
16264	II	Yes
17071	II	Yes
16009	II	Yes
12836	II	Yes
17089	II	Yes
17067	II	Yes
14371	II	Yes
17022	II	Yes
16423	II	Yes
17103	II	Yes
16348	II	Yes
16003	II	Yes
13672	II	Yes
16647	II	Yes
17174	II	Yes
16023	II	Yes
12471	II	Yes
16757	II	Yes
17098	II	Yes

14542	II	Yes
12622	II	Yes
16019	II	Yes
17069	II	Yes
15981	II	Yes
16553	II	Yes
14333	II	Yes
17080	II	Yes
16514	II	Yes
12047	II	Yes
16497	II	Yes
13308	II	Yes
13559	II	Yes
17040	II	Yes
16654	II	Yes
11637	II	Yes
16542	II	Yes
16168	II	Yes
14022	II	Yes
16683	II	Yes
16414	II	Yes
12270	II	Yes
17085	II	Yes
15993	II	Yes
16787	II	Yes
17093	II	Yes
17057	II	Yes
16366	IIIb	Yes
16082	IIIb	Yes
14137	IIIb	Yes
16045	IIIb	Yes
16532	IIIb	Yes
14921	IIIb	Yes
16300	IIIb	Yes
14782	IIIb	Yes
17059	IIIb	Yes
16845	IIIb	Yes
16910	IIIb	Yes
16073	IIIb	Yes
16786	IIIb	Yes
16861	IIIb	Yes
16327	IIIb	Yes
16729	IIIb	Yes
16826	IIIb	Yes
17170	IIIb	Yes
16818	IIIb	Yes
16214	IIIb	Yes
12250	IIIb	Yes

12933	IIIb	Yes
16801	IIIb	Yes
16425	IIIb	Yes
17018	IIIb	Yes
11783	IIIb	Yes
16296	IIIb	Yes
16234	IIIb	Yes
16304	IIIb	Yes
16292	IIIb	Yes
13543	IIIb	Yes
16583	IIIb	Yes
16661	IIIb	Yes
12397	IIIb	Yes
16328	IIIb	Yes
16022	IIIb	Yes
16584	IIIb	Yes
12454	IIIb	Yes
16802	IIIb	Yes
16060	IIIb	Yes
12715	IIIb	Yes
16652	IIIb	Yes
14121	IIIb	Yes
16050	IIIb	Yes
14179	IIIb	Yes
16293	IIIb	Yes
16603	IIIb	Yes
16232	IIIb	Yes
16459	IIIb	Yes
16797	IIIb	Yes
12028	IIIb	Yes
16279	IIIb	Yes
16834	IIIb	Yes
16324	IIIb	Yes
17146	IIIb	Yes
11766	IIIb	Yes
16294	IIIb	Yes
12027	IIIb	Yes
16307	IIIb	Yes
16440	IIIb	Yes
17060	IIIb	Yes
11733	IIIb	Yes
16628	IIIb	Yes
14530	IIIb	Yes
16511	IIIb	Yes
12486	IIIb	Yes
16790	IIIb	Yes
16305	IIIb	Yes
16054	IIIb	Yes

17075	IIIb	Yes	
15117	IIIb	Yes	
16302	IIIb	Yes	
16906	IIIb	Yes	
16911	IIIb	Yes	
11765	IIIb	Yes	
17037	IIIb	Yes	
16018	IIIb	Yes	
16464	IIIb	Yes	
16046	IIIb	Yes	
16725	IIIb	Yes	
11973	IIIb	Yes	
16035	IIIb	Yes	
16515	IIIb	Yes	
12843	IIIb	Yes	
16726	IIIb	Yes	
13856	IIIb	Yes	
16051	IIIb	Yes	
11631	IIIb	Yes	
16849	IIIb	Yes	
16731	IIIb	Yes	
16030	IIIb	Yes	
15348	IIIb	Yes	
15959	IV	Yes	Yes
15958	IV	Yes	Yes
16055	IV	Yes	
16032	IV	Yes	
11990	IV	Yes	
16833	IV	Yes	
16738	IV	Yes	
17127	IV	Yes	
16761	IV	Yes	
16980	IV	Yes	
16718	IV	Yes	
16842	IV	Yes	
13403	IV	Yes	
12602	IV	Yes	
16287	IV	Yes	
16033	IV	Yes	
16989	IV	Yes	
12661	IV	Yes	
13295	IV	Yes	
16226	IV	Yes	
16064	IV	Yes	
14367	IV	Yes	
16607	IV	Yes	
16709	IV	Yes	
16699	IV	Yes	

14075	IV	Yes
16873	IV	Yes
16721	IV	Yes
16865	IV	Yes
16748	IV	Yes
12654	IV	Yes
16715	IV	Yes
16903	IV	Yes
16759	IV	Yes
16527	IV	Yes
16356	IV	Yes
13464	IV	Yes
16703	IV	Yes
16689	IV	Yes
12618	IV	Yes
16796	IV	Yes
16262	IV	Yes
13471	IV	Yes
16788	IV	Yes
14134	IV	Yes
12462	IV	Yes
16357	IV	Yes
14195	IV	Yes
16227	IV	Yes
16365	IV	Yes
12846	IV	Yes
13356	IV	Yes
16231	IV	Yes
12474	IV	Yes
15976	IV	Yes
16867	IV	Yes
13696	IV	Yes
16575	IV	Yes
12930	IV	Yes
16065	IV	Yes
16682	IV	Yes
13371	IV	Yes
16747	IV	Yes
16685	IV	Yes
12954	IV	Yes
14131	IV	Yes
16716	IV	Yes
16649	IV	Yes
16836	IV	Yes
14017	IV	Yes
16713	IV	Yes
15977	IV	Yes
16576	IV	Yes

16034	IV	Yes		
16360	IV	Yes		
13412	IV	Yes		
16646	IV	Yes		
16485	IV	Yes		
16692	IV	Yes		
13449	IV	Yes		
14444	IV	Yes		
16775	IV	Yes		
16785	IV	Yes		
13369	IV	Yes		
16875	IV	Yes		
12736	IV	Yes		
14419	IV	Yes		
13461	IV	Yes		
16419	IV	Yes		
16312	IV	Yes		
16310	IV	Yes		
16706	IV	Yes		
14378	IV	Yes		
17095	IX	Yes		Yes
16815	*S. arizonae*	Yes		
15377	*S. arizonae*	Yes		
17139	*S. arizonae*	Yes		
13863	*S. arizonae*	Yes		
13607	*S. arizonae*	Yes		
14926	*S. arizonae*	Yes		
13665	*S. arizonae*	Yes		
11635	*S. arizonae*	Yes		
16744	*S. arizonae*	Yes		
16840	*S. arizonae*	Yes		
16695	*S. arizonae*	Yes		
16806	*S. arizonae*	Yes		
16632	*S. arizonae*	Yes		
16610	*S. arizonae*	Yes		
13914	*S. arizonae*	Yes		
16098	*S. arizonae*	Yes		
15975	*S. arizonae*	Yes		
16592	*S. arizonae*	Yes		
16281	*S. arizonae*	Yes		
16299	*S. arizonae*	Yes		
16165	*S. arizonae*	Yes		
16512	*S. arizonae*	Yes		
16779	*S. arizonae*	Yes		
16830	*S. arizonae*	Yes		
16273	*S. arizonae*	Yes		
16880	*S. arizonae*	Yes		
16580	*S. arizonae*	Yes		

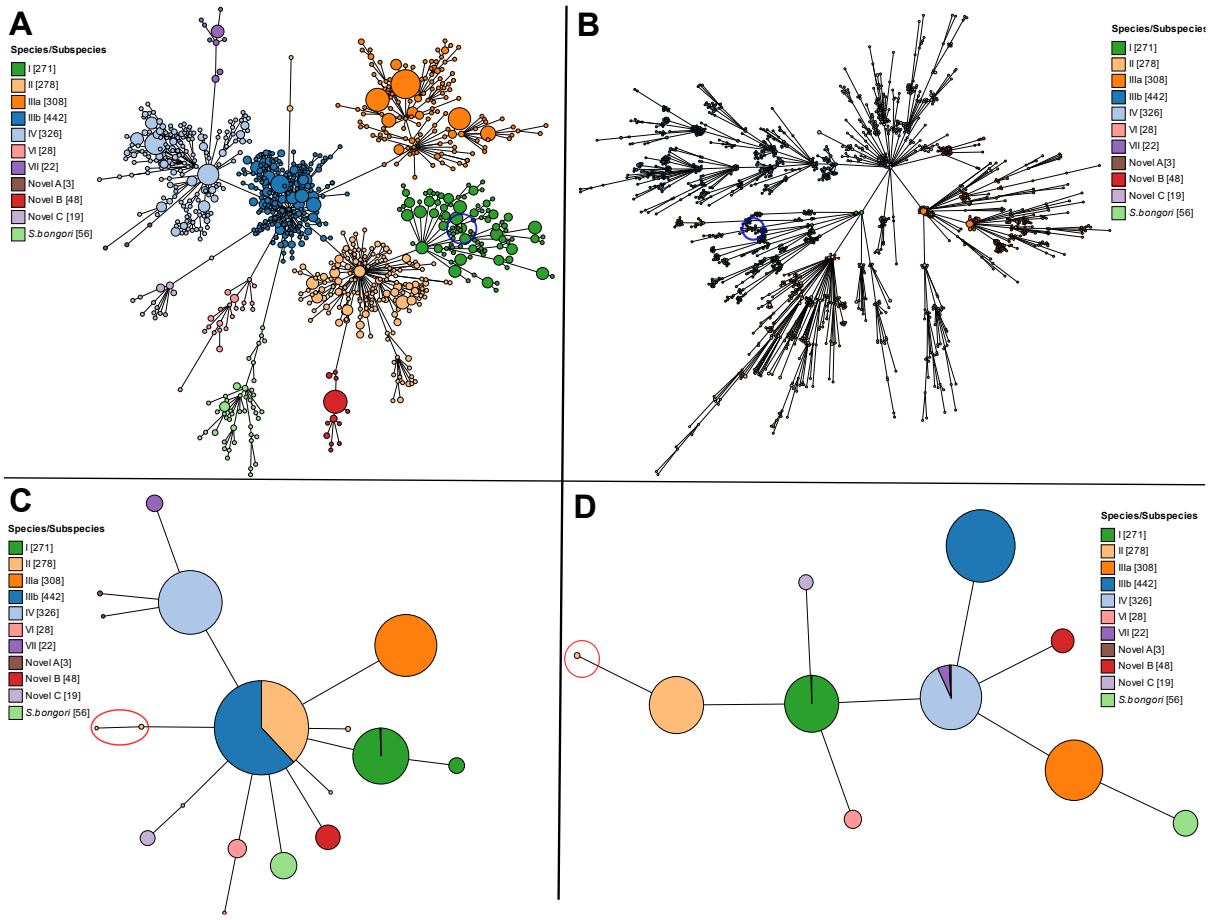
16506	*S. arizonae*	Yes
13961	*S. arizonae*	Yes
16078	*S. arizonae*	Yes
16700	*S. arizonae*	Yes
16217	*S. arizonae*	Yes
16889	*S. arizonae*	Yes
16798	*S. arizonae*	Yes
12325	*S. arizonae*	Yes
14122	*S. arizonae*	Yes
16031	*S. arizonae*	Yes
16237	*S. arizonae*	Yes
16518	*S. arizonae*	Yes
16517	*S. arizonae*	Yes
16752	*S. arizonae*	Yes
12837	*S. arizonae*	Yes
13630	*S. arizonae*	Yes
16676	*S. arizonae*	Yes
16655	*S. arizonae*	Yes
16708	*S. arizonae*	Yes
16847	*S. arizonae*	Yes
16672	*S. arizonae*	Yes
16839	*S. arizonae*	Yes
16690	*S. arizonae*	Yes
15039	*S. arizonae*	Yes
16763	*S. arizonae*	Yes
16513	*S. arizonae*	Yes
12535	*S. arizonae*	Yes
16871	*S. arizonae*	Yes
13972	*S. arizonae*	Yes
15118	*S. arizonae*	Yes
16609	*S. arizonae*	Yes
16733	*S. arizonae*	Yes
17025	*S. arizonae*	Yes
16249	*S. arizonae*	Yes
16582	*S. arizonae*	Yes
16714	*S. arizonae*	Yes
13460	*S. arizonae*	Yes
16595	*S. arizonae*	Yes
16409	*S. arizonae*	Yes
16773	*S. arizonae*	Yes
16675	*S. arizonae*	Yes
16615	*S. arizonae*	Yes
16291	*S. arizonae*	Yes
16894	*S. arizonae*	Yes
12886	*S. arizonae*	Yes
17171	*S. arizonae*	Yes
15999	*S. arizonae*	Yes
16825	*S. arizonae*	Yes

16411	*S. arizonae*	Yes		
12623	*S. arizonae*	Yes		
16533	*S. arizonae*	Yes		
16557	*S. arizonae*	Yes		
16760	*S. arizonae*	Yes		
15018	*S. arizonae*	Yes		
12855	*S. arizonae*	Yes		
16776	*S. arizonae*	Yes		
16887	*S. arizonae*	Yes		
16106	*S. arizonae*	Yes		
16574	*S. arizonae*	Yes		
13446	*S. arizonae*	Yes		
16401	*S. arizonae*	Yes		
13965	*S. arizonae*	Yes		
16856	*S. arizonae*	Yes		
16039	*S. arizonae*	Yes		
16616	*S. arizonae*	Yes		
16693	*S. arizonae*	Yes		
15971	*S.bongori*	Yes		Yes (primary)
16771	*S.bongori*	Yes		
16269	*S.bongori*	Yes		
16449	*S.bongori*	Yes		
15140	*S.bongori*	Yes		
16549	*S.bongori*	Yes		
14904	*S.bongori*	Yes		
16587	*S.bongori*	Yes		
16222	*S.bongori*	Yes		
13799	*S.bongori*	Yes		
16274	*S.bongori*	Yes		
16223	*S.bongori*	Yes		
16265	*S.bongori*	Yes		
12887	*S.bongori*	Yes		
12049	*S.bongori*	Yes		
16569	*S.bongori*	Yes		
13189	*S.bongori*	Yes		
16109	*S.bongori*	Yes		
17142	*S.bongori*	Yes		
16812	*S.bongori*	Yes		
17138	*S.bongori*	Yes		
15972	*S.bongori*	Yes		
16152	VI	Yes		Yes (secondary)
12496	VI	Yes		
12479	VI	Yes		
16767	VI	Yes		
16827	VI	Yes		
13620	VI	Yes		
14197	VI	Yes		

16578	VI	Yes				
16220	VI	Yes				
15967	X	Yes				
12478	X	Yes				
16080	X	Yes				
12664	VII		Yes	Yes (secondary)	Yes (secondary)	
16552	VII		Yes			
17191	I			Yes (primary)		
17190	I			Yes (secondary)		
17189	I			Yes (secondary)		
16394	II			Yes (primary)		
16405	II			Yes (secondary)		
16389	IIIb			Yes (primary)		
16391	IV			Yes (primary)		
15996	IX			Yes (primary)	Yes (secondary)	Yes
16153	IX			Yes (secondary)		
16406	*S. arizonae*			Yes (primary)		
16400	*S. arizonae*			Yes (secondary)		
16353	*S.bongori*			Yes (secondary)		Yes
17137	VI			Yes (secondary)		Yes
16393	VI			Yes (primary)		
16108	VII			Yes (primary)		Yes
16160	X			Yes (primary)		
16132	I				Yes (primary)	
16130	I				Yes (secondary)	
16131	I				Yes (secondary)	
18436	I					Yes
18437	I					Yes
16134	II				Yes (secondary)	
16341	II					Yes
15963	II					Yes
17172	I/II					Yes
16137	IIIb				Yes (primary)	
16138	IIIb				Yes (secondary)	
15962	IIIb					Yes
15960	IIIb					Yes
16139	IV				Yes (primary)	
16140	IV				Yes (secondary)	

16135	*S. arizonae*	Yes (primary)	
16136	*S. arizonae*	Yes (secondary)	
17148	*S. arizonae*		Yes
17159	*S. arizonae*		Yes
16150	*S. bongori*	Yes (secondary)	
16021	*S. bongori*		Yes
16151	VI	Yes (primary)	
12609	VII	Yes (primary)	
Not_in_PubMLST	VIII		Yes
16146	X	Yes (secondary)	
17108	X		Yes

Minimal Spanning Trees calculated using GrapeTree of all isolates (A) calculated using rMLST (B) calculated using cgMLST (C) calculated using rMLST and collapsed to 20/51 loci different and (D) calculated using cgMLST and collapsed to 2640 /2750 loci different



Minimal Spanning Trees created using the GrapeTree algorithm, using all 1801 isolates. This dataset is composed of 271 subspecies I, 278 II, 308 IIIa, 442 IIIb, 326 IV, 28 VI, 22 VII, 3 Novel A, 48 Novel B, 19 Novel C and 56 *S. bongori* and is labelled according to the original metadata. These isolates cover all non-subspecies isolates and a subset of the most common *S. enterica* subspecies I isolates.

A: Minimal Spanning Tree created using GrapeTree on the rMLST loci. All of the isolates clustered within their respective subspecies, with the exception of SAL_MA5841AA (node circled in blue), which was biochemically identified as subspecies II but genetically as subspecies I. The results of the rMLST tree were highly congruent with the cgMSLT tree, suggesting that the increased time taken for a cgMLST analysis is not required for subspeciation analysis.

B: Minimal Spanning Tree created using GrapeTree on the cgMLST loci. All of the isolates clustered within their respective subspecies, with the exception of SAL_MA5841AA (node circled in blue), which was biochemically identified as subspecies II but genetically as subspecies I. The results between the cgMLST and rMLST trees were highly congruent.

C: Minimal Spanning Tree created using GrapeTree on the rMLST loci of 1530 isolates and collapsed to differences of 20/51 loci, at this point the major subspecies II grouping merged with the subspecies I isolates. This suggests that most isolates can be grouped into a specific subspecies when collapsed to 19/51 loci, within this analysis. Isolates that did not cluster with any other subspecies but formed a cluster of three or more isolates were ideal candidates for novel subspecies. This led to the identification of novel subspecies XI (red circle). The other isolates that did not cluster with subspecies II were not of three or more isolates, however searches in Enterobase for further isolates closely related to them were conducted and no similar isolate were found.

D: Minimal Spanning Tree created using GrapeTree on the cgMLST loci of 1530 isolates and collapsed to differences of 2640/2750 loci, at this point both the subspecies VII and Novel A (VIII) subspecies groups merged with the subspecies IV isolates. At 2584 no subspecies were merged together, suggesting that a more relaxed cut-off of 2550 differences would group the majority of isolates from the same subspecies together, and no isolates from different subspecies would group together. Isolates that did not cluster with any other subspecies but formed a cluster of multiple isolates were ideal candidates for novel subspecies. This led to the identification of novel subspecies XI (red circle).

A maximum-likelihood tree based on the rMLST loci of 569 representative isolates

Maximum-Likelihood tree of dataset A isolates. The presence of distinct clades supported the findings of novel subspecies and the reclassification of subspecies IIIa to *S. arizonae*, as, like *S. bongori,* it was also ancestral to *S. enterica*. Using MAFFT rMLST profiles were aligned and exported from BIGSdb, these profiles were then used to create a Maximum-Likelihood tree using muscle with 100 bootstrap replications using the Kimura 2-parameter model[46]. All bootstrap values over 0.8 are displayed, as all species and subspecies groups were supported by a bootstrap of over 0.8 (0.82 – 1.00). The Maximum-Likelihood tree was highly congruent to the Neighbour-Joining trees, showing exactly the same species and subspecies clades, suggesting that the use of nucleotide data provided no extra meaningful information over allelic data in this circumstance. Isolate SAL_BA7507AA continued to cluster with subspecies XI instead of subspecies II.

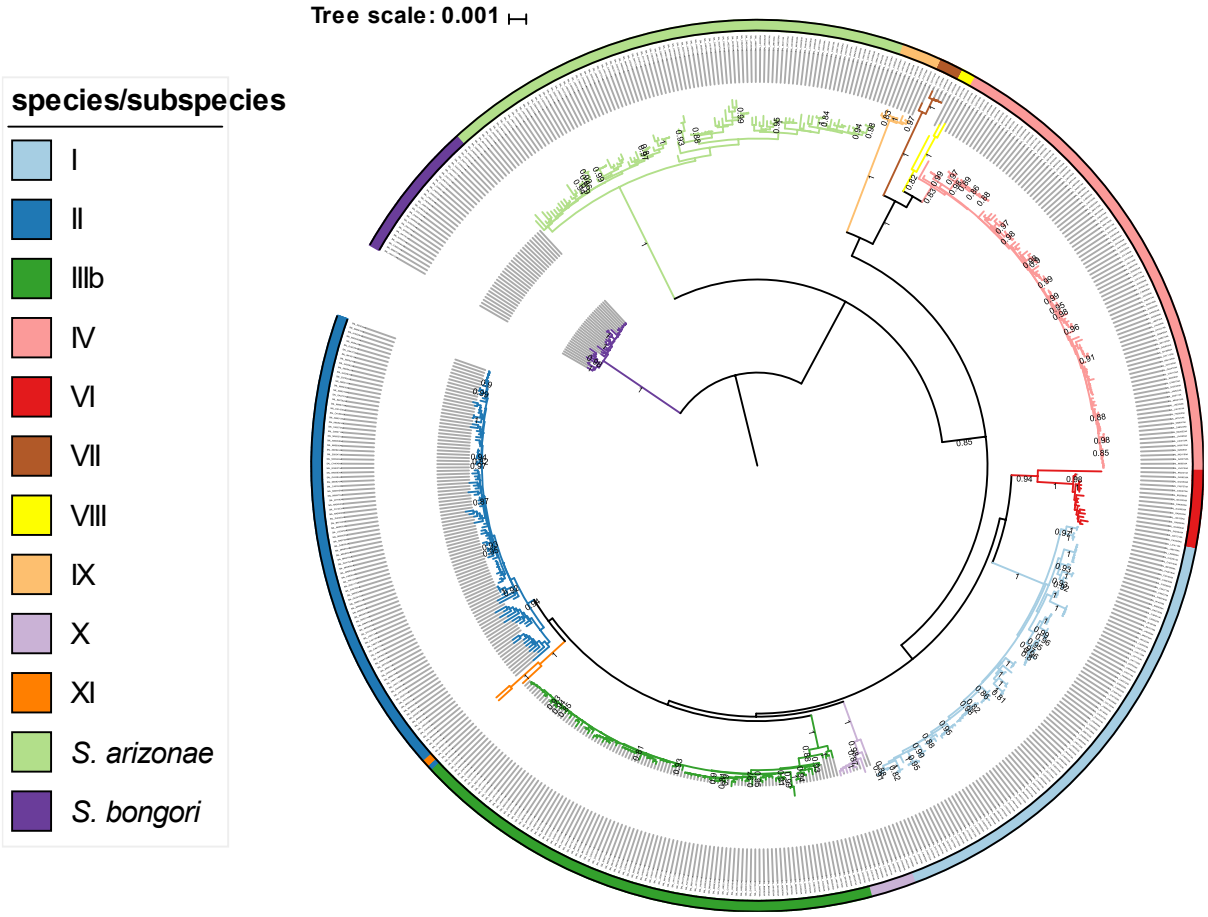


Table of all type strain and prospective type strains isolates used for ANI analyses (Chapter Five)

PubMLST_id	NCTC_accession	subspecies	serovar	Type Strain	Proposed Type strain
17191	NCTC12416	I	typhimurium	Yes	
17190	NCTC20107	I	typhi	Yes	
17189	NCTC20044	I	oranienburg	Yes	
16394	NCTC5773	II		Yes	
16405	NCTC8273	II		Yes	
16389	NCTC10060	IIIb		Yes	
16373	NCTC10047	IIIb		Yes	
16391	NCTC12418	IV		Yes	
16402	NCTC7318	IV		Yes	
15996		IX			Yes
16153		IX			Yes
16406	NCTC8297	*S. arizonae*		Yes	
16400	NCTC7306	*S. arizonae*		Yes	
16392	NCTC12419	*S.bongori*		Yes	
16393	NCTC12420	VI		Yes	
16108		VII			Yes
16111		VIII			Yes
16160		X			Yes
15989		X			Yes
16002		XI			Yes

ANI analysis of (A) randomly selected isolates of each species and subspecies using wgs (B) ANI analysis of randomly selected isolates of each species and subspecies using cgMLST (C) ANI analysis of randomly selected isolates of each species and subspecies using rMLST

A) Whole Genome

	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	S. arizonae	S. bongori
I	98.41											
II	95.98	99.28										
IIIb	94.95	96.12	99.48									
IV	94.96	95.67	94.75	99.32								
VI	95.63	96.08	95.27	94.78	99.51							
VII	93.66	94.07	93.83	96.61	93.58	99.5						
VIII	95.94	95.58	94.83	97.15	94.85	96.27	99.94					
IX	94.65	95.26	94.87	94.05	94.67	93.14	94.23	99.73				
X	95.29	96.16	95.67	94.83	95.33	93.68	94.74	94.82	98.91			
XI	95.78	97.55	95.96	95.28	95.85	94.03	95.23	95.09	95.94	98.79		
S. arizonae	93.47	93.76	93.82	93.26	93.1	92.94	93.31	92.92	93.43	93.61	99.47	
S. bongori	89.96	89.79	89.85	89.45	89.57	89.35	89.59	89.68	89.6	89.98	88.99	99.3

B) cgMLST

	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	S. arizonae	S. bongori
I	98.77											
II	96.92	99.49										
IIIb	96.25	96.97	99.68									
IV	95.96	96.59	96.12	99.62								
VI	96.54	96.97	96.27	96.02	99.67							
VII	94.6	95.3	95.07	96.96	94.83	99.57						
VIII	96.84	96.4	95.91	97.47	95.96	96.5	99.96					
IX	95.58	96.24	95.86	95.34	95.68	94.32	95.2	99.86				
X	96.42	96.96	96.69	95.96	96.4	94.97	95.95	96.05	99.35			
XI	96.64	98.11	96.92	96.51	96.79	95.1	96.2	96.12	96.87	99.17		
S. arizonae	94.56	94.89	94.8	94.54	94.49	94.13	94.71	94.02	94.66	95	99.61	
S. bongori	90.8	91.1	91.14	90.73	90.74	90.36	90.69	90.77	90.85	90.93	90.42	99.54

C) rMLST

	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	S. arizonae	S. bongori
I	99.8											
II	99.37	99.91										
IIIb	99.21	99.53	99.91									
IV	98.88	99.13	99.13	99.84								
VI	99.16	99.41	99.35	98.98	99.93							
VII	98.58	98.73	98.75	99.19	98.61	99.81						
VIII	99.08	98.98	98.97	99.42	98.85	99.02	99.8					
IX	98.76	98.94	98.89	98.8	98.78	98.47	98.78	99.94				
X	99.28	99.48	99.42	99.02	99.27	98.6	98.92	98.85	99.86			
XI	99.11	99.36	99.24	98.91	99.19	98.55	98.83	98.77	99.23	99.79		
S. arizonae	98.58	98.65	98.64	98.58	98.48	98.42	98.45	98.33	98.59	98.44	99.96	
S. bongori	98.16	98.36	98.42	98.11	98.38	98.03	98.05	98	98.33	98.23	98.02	99.94

ANI analyses of randomly selected isolates for each species and subspecies. Each isolate was compared to an isolate of all the other species or subspecies and with a secondary isolate that belonged to the same species or subspecies using the OrthoANI algorithm. Isolates of the same species or subspecies were always more closely related than isolates from different species or subspecies. *S. arizonae* and *S. bongori* were most distantly related to isolates from *S. enterica*, supporting their classification as different species. Results were highly congruent between randomly selected isolates and the chosen type strains.

A: ANI analysis of random isolates using wgs. All comparisons of species and subspecies against *S. bongori* scored below 90% similarity, comparisons against *S. arizonae* also all

scored below the 95% cut-off, although the comparisons were all higher, supporting the reclassification of subspecies IIIa as a species. Comparisons between the other subspecies ranged between 93.14% - 97.55%. On the other hand, comparisons within the subspecies ranged from 98.41% - 99.94%. These differences supported the identification of the novel subspecies. These results were highly congruent with the results from the type strain analysis.

B: ANI analysis of random isolates using cgMLST. The cgMLST analysis was congruent with the wgs ANI results and with the cgMLST analysis of type strains. *S. bongori* and *S. arizonae* were still lower than the 95% threshold, supporting the reclassification of subspecies IIIa as a species. Comparisons between the other subspecies (94.32% - 98.11%) were again lower than comparisons within subspecies (99.8% - 99.96%).

C: ANI analysis of random isolates using the rMLST loci. The patterns observed within the rMLST analysis congruent with the cgMLST and wgs analyses. This suggested that the patterns observed within the relatedness of the species and subspecies persisted down to the rMLST loci. The results were congruent with those observed using the type strains.

ANI analysis using both randomly selected representatives of subspecies and type strain of (A) isolate SAL_BA7507AA and (B) isolate SAL_MA5841AA

cgMLST_random

	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	*S. arizonae*	*S. bongori*
SAL_BA7507AA	96.95	98.58	96.97	96.59	96.87	95.19	96.31	96.18	96.88	98.31	94.93	91.12

cgMLST_type

	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	*S. arizonae*	*S. bongori*
SAL_BA7507AA	96.87	98.32	97.03	96.57	96.78	95.14	96.3	96.18	96.88	98.24	94.86	91.13

wgs_random

	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	*S. arizonae*	*S. bongori*
SAL_BA7507AA	96	97.99	95.98	95.52	95.88	94.02	95.36	95.17	95.87	97.87	93.72	89.88

wgs_type

	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	*S. arizonae*	*S. bongori*
SAL_BA7507AA	96.07	97.65	96.08	95.44	96.01	94	95.46	95.07	95.94	97.69	93.69	89.78

cgMLST_random

	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	*S. arizonae*	*S. bongori*
SAL_MA5841AA	99.99	96.93	96.31	95.9	96.49	94.71	96.78	95.65	96.27	96.67	94.52	90.99

cgMLST_type

	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	*S. arizonae*	*S. bongori*
SAL_MA5841AA	99.99	96.89	96.13	95.96	96.41	94.65	96.73	95.58	96.38	96.63	94.38	91.12

wgs_type

	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	*S. arizonae*	*S. bongori*
SAL_MA5841AA	99.89	96.08	95.14	94.86	95.59	93.67	95.8	94.37	95.19	95.7	93.42	89.84

wgs_random

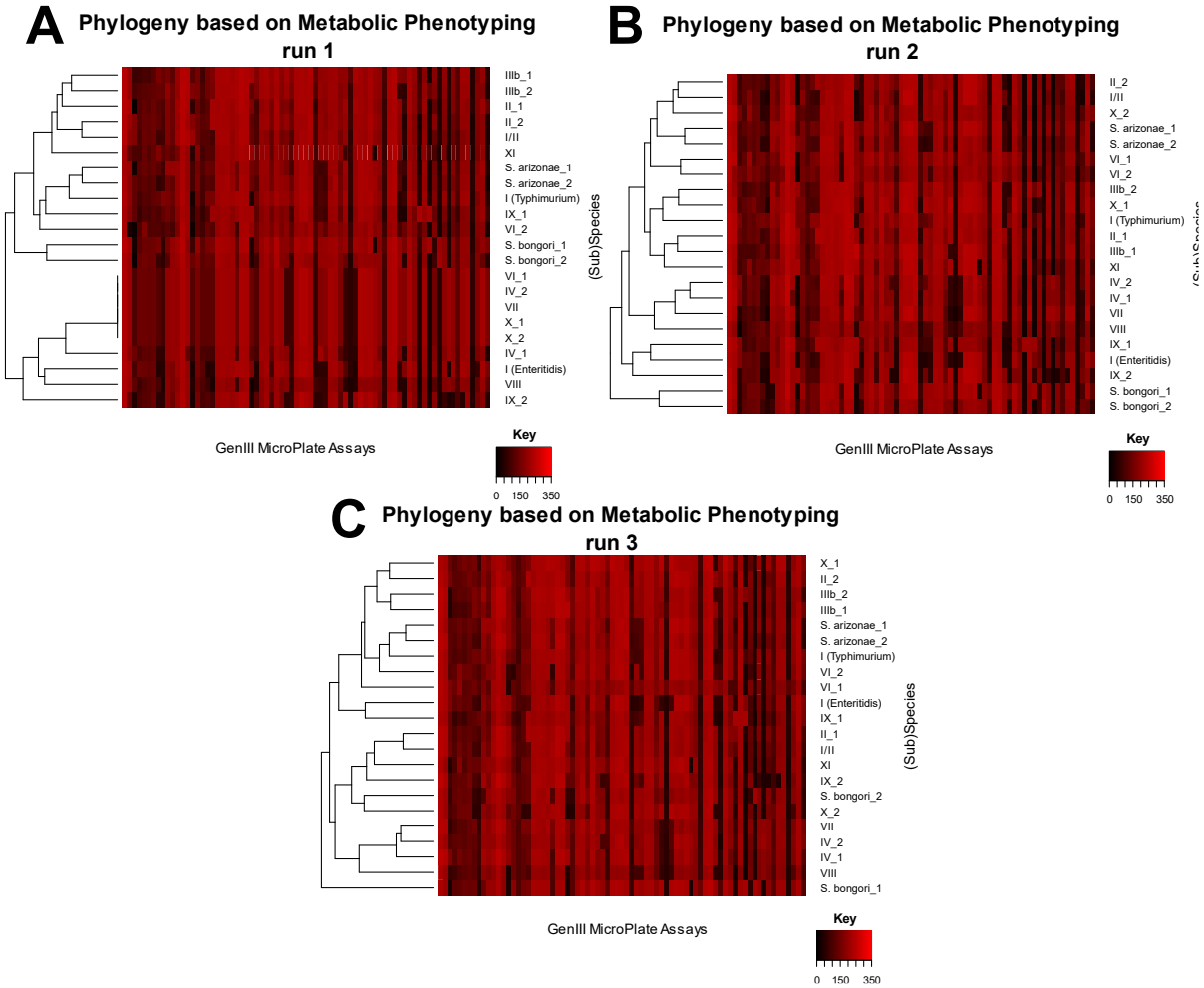
	I	II	IIIb	IV	VI	VII	VIII	IX	X	XI	*S. arizonae*	*S. bongori*
SAL_MA5841AA	99.98	96.1	94.96	94.98	95.67	93.61	95.98	94.55	95.37	95.74	93.32	89.95

ANI analyses of the isolates within this study which did not cluster consistently. These isolates were compared to representatives of the other subspecies to see which they were most closely related to, in order to help determine their subspecies.

A: ANI analysis comparing the WGS of SAL_BA7507AA with the WGS of representative isolates for each other species and subspecies. SAL_BA7507AA was most closely related to subspecies II and XI, however it was less related to these subspecies than isolates within these subspecies are to each other. This suggests that SAL_BA7507AA is either representative of a further novel subspecies or represents a midpoint between these two subspecies.

B: ANI analysis comparing the WGS of SAL_MA5841AA with the WGS of representative isolates for each other species and subspecies. SAL_MA5841AA was by far most closely related to subspecies I, when compared to either the type strains or randomly selected isolates SAL_MA5841AA was more than 99.8% ANI. This suggests that SAL_MA5841AA belongs to subspecies I. This isolate was not particularly closely related to any of the other subspecies.

Dendrograms based on metabolic phenotyping using the Biolog GenIII MicroPlate assays of (A) run 1 (B) run 2 and (C) run 3



Dendrograms based on metabolic phenotyping from the Biolog GenIII MicroPlate assays from which the averages were taken. The results show similarities and reasonable congruence between all three runs, therefore no runs were removed when calculating the averages. Run 1 Is shown in A, run 2 is shown in B and run 3 is shown in C.

Table showing all isolates used within the Australian analysis (Chapter Six)

id	country	continent	Region	Analysis
1760606	Malawi	Africa		100perContinent
1774606	Uganda	Africa		100perContinent
1774607	Uganda	Africa		100perContinent
1774604	Mauritius	Africa		100perContinent
1774605	Mauritius	Africa		100perContinent
1738606	Mauritius	Africa		100perContinent
1738605	Mauritius	Africa		100perContinent
1743000	Mauritius	Africa		100perContinent
1738604	Mauritius	Africa		100perContinent
1742609	Mauritius	Africa		100perContinent
1773605	Congo [DRC]	Africa		100perContinent
1773607	Mauritius	Africa		100perContinent
1773608	Nigeria	Africa		100perContinent
1776606	Ethiopia	Africa		100perContinent
1776607	Ethiopia	Africa		100perContinent
1776608	Ethiopia	Africa		100perContinent
1781606	Canada	North America		100perContinent
1781607	Canada	North America		100perContinent
1781608	Canada	North America		100perContinent
1781609	Canada	North America		100perContinent
1782000	Canada	North America		100perContinent
1782101	Canada	North America		100perContinent
1782102	Canada	North America		100perContinent
1782103	Canada	North America		100perContinent
1782104	Canada	North America		100perContinent
1782105	Canada	North America		100perContinent
1783303	Canada	North America		100perContinent
1825303	Canada	North America		100perContinent
1825304	Canada	North America		100perContinent
1825307	Canada	North America		100perContinent
1825308	Canada	North America		100perContinent
1825309	Canada	North America		100perContinent

1776	Ethiopia	Africa	100perContinent	1826	Canada	North America	100perContinent
1757	Ethiopia	Africa	100perContinent	1826	Canada	North America	100perContinent
1757	Ethiopia	Africa	100perContinent	1826	Canada	North America	100perContinent
1757	Ethiopia	Africa	100perContinent	1827	USA	North America	100perContinent
1757	Ethiopia	Africa	100perContinent	1863	USA	North America	Continent Comparison
1757	Ethiopia	Africa	100perContinent	1859	USA	North America	Continent Comparison
1824	Ethiopia	Africa	100perContinent	1860	USA	North America	Continent Comparison
1756	Ethiopia	Africa	100perContinent	1860	USA	North America	Continent Comparison
1824	Ethiopia	Africa	100perContinent	1859	USA	North America	Continent Comparison
1824	Ethiopia	Africa	100perContinent	1859	USA	North America	Continent Comparison
1824	Ethiopia	Africa	100perContinent	1863	USA	North America	Continent Comparison
1756	Ethiopia	Africa	100perContinent	1864	USA	North America	Continent Comparison
1756	Ethiopia	Africa	100perContinent	1862	USA	North America	Continent Comparison
1756	Ethiopia	Africa	100perContinent	1861	USA	North America	Continent Comparison
1756	Ethiopia	Africa	100perContinent	1863	USA	North America	Continent Comparison
1756	Ethiopia	Africa	100perContinent	1862	USA	North America	Continent Comparison
1756	Ethiopia	Africa	100perContinent	1859	USA	North America	Continent Comparison
1756	Ethiopia	Africa	100perContinent	1856	Canada	North America	Continent Comparison
1756	Ethiopia	Africa	100perContinent	1857	Canada	North America	Continent Comparison

1756				1857			
3	Ethiopia	Africa	100perContinent	9	Canada	North America	Continent Comparison
1757				1856			
6	Ethiopia	Africa	100perContinent	1	Canada	North America	Continent Comparison
1782				1860			
6	Malawi	Africa	100perContinent	9	USA	North America	Continent Comparison
1758				1862			
0	South Africa	Africa	100perContinent	5	USA	North America	Continent Comparison
1791				1862			
0	Uganda	Africa	100perContinent	9	USA	North America	Continent Comparison
1789				1860			
1	Uganda	Africa	100perContinent	0	USA	North America	Continent Comparison
1789				1862			
0	Uganda	Africa	100perContinent	1	USA	North America	Continent Comparison
1788				1859			
9	Uganda	Africa	100perContinent	7	USA	North America	Continent Comparison
1788				1861			
8	Uganda	Africa	100perContinent	0	USA	North America	Continent Comparison
1789				1862			
9	Uganda	Africa	100perContinent	6	USA	North America	Continent Comparison
1789				1862			
8	Uganda	Africa	100perContinent	8	USA	North America	Continent Comparison
1790				1864			
0	Uganda	Africa	100perContinent	1	USA	North America	Continent Comparison
1790				1854			
2	Uganda	Africa	100perContinent	9	Canada	North America	Continent Comparison
1790				1860			
1	Uganda	Africa	100perContinent	4	USA	North America	Continent Comparison
1789				1863			
7	Uganda	Africa	100perContinent	7	USA	North America	Continent Comparison
1790				1862			
8	Uganda	Africa	100perContinent	0	USA	North America	Continent Comparison
1790				1861			
7	Uganda	Africa	100perContinent	5	USA	North America	Continent Comparison
1790				1859			
5	Uganda	Africa	100perContinent	4	USA	North America	Continent Comparison
1790				1861			
6	Uganda	Africa	100perContinent	9	USA	North America	Continent Comparison

1790	Uganda	Africa	100perContinent	1861	USA	North America	Continent Comparison
1755	Malawi	Africa	100perContinent	1863	USA	North America	Continent Comparison
1755	Malawi	Africa	100perContinent	1862	USA	North America	Continent Comparison
1755	Malawi	Africa	100perContinent	1864	USA	North America	Continent Comparison
1755	Malawi	Africa	100perContinent	1861	USA	North America	Continent Comparison
1740	Thailand	Asia	100perContinent	1863	USA	North America	Continent Comparison
1748	Thailand	Asia	100perContinent	1859	USA	North America	Continent Comparison
1749	Thailand	Asia	100perContinent	1863	USA	North America	Continent Comparison
1741	Thailand	Asia	100perContinent	1863	USA	North America	Continent Comparison
1750	Thailand	Asia	100perContinent	1861	USA	North America	Continent Comparison
1742	Thailand	Asia	100perContinent	1861	USA	North America	Continent Comparison
1743	Thailand	Asia	100perContinent	1860	USA	North America	Continent Comparison
1752	Saudi Arabia	Asia	100perContinent	1860	USA	North America	Continent Comparison
1736	Turkey	Asia	100perContinent	1859	USA	North America	Continent Comparison
1739	Iran	Asia	100perContinent	1863	USA	North America	Continent Comparison
1749	Taiwan	Asia	100perContinent	1860	USA	North America	Continent Comparison
1749	Taiwan	Asia	100perContinent	1863	USA	North America	Continent Comparison
1743	Pakistan	Asia	100perContinent	1863	USA	North America	Continent Comparison
1754	China	Asia	100perContinent	1860	USA	North America	Continent Comparison

1757	Thailand	Asia	100perContinent	1862	USA	North America	Continent Comparison
1740	Vietnam	Asia	100perContinent	1860	USA	North America	Continent Comparison
1740	India	Asia	100perContinent	1858	Canada	North America	Continent Comparison
1741	China	Asia	100perContinent	1856	Canada	North America	Continent Comparison
1795	China	Asia	100perContinent	1854	Canada	North America	Continent Comparison
1740	Sri Lanka	Asia	100perContinent	1854	Canada	North America	Continent Comparison
1741	India	Asia	100perContinent	1854	Canada	North America	Continent Comparison
1742	China	Asia	100perContinent	1854	Canada	North America	Continent Comparison
1738	China	Asia	100perContinent	1854	Canada	North America	Continent Comparison
1741	Taiwan	Asia	100perContinent	1854	Canada	North America	Continent Comparison
1749	India	Asia	100perContinent	1854	Canada	North America	Continent Comparison
1752	Vietnam	Asia	100perContinent	1855	Canada	North America	Continent Comparison
1754	India	Asia	100perContinent	1855	Canada	North America	Continent Comparison
1754	India	Asia	100perContinent	1855	Canada	North America	Continent Comparison
1740	South Korea	Asia	100perContinent	1855	Canada	North America	Continent Comparison
1739	Indonesia	Asia	100perContinent	1855	Canada	North America	Continent Comparison
1742	Vietnam	Asia	100perContinent	1855	Canada	North America	Continent Comparison
1820	China	Asia	100perContinent	1855	Canada	North America	Continent Comparison
1742	Bangladesh	Asia	100perContinent	1855	Canada	North America	Continent Comparison

1754	Bangladesh	Asia	100perContinent
1773	China	Asia	100perContinent
1758	Pakistan	Asia	100perContinent
1758	Pakistan	Asia	100perContinent
1753	China	Asia	100perContinent
1754	Bangladesh	Asia	100perContinent
1775	China	Asia	100perContinent
1757	Burma	Asia	100perContinent
1758	Bangladesh	Asia	100perContinent
1775	Taiwan	Asia	100perContinent
1783	China	Asia	100perContinent
1783	Turkey	Asia	100perContinent
1822	China	Asia	100perContinent
1822	China	Asia	100perContinent
1738	Syria	Asia	100perContinent
1738	China	Asia	100perContinent
1738	Turkey	Asia	100perContinent
1742	Turkey	Asia	100perContinent
1738	India	Asia	100perContinent
1855	Canada	North America	Continent Comparison
1855	Canada	North America	Continent Comparison
1856	Canada	North America	Continent Comparison
1856	Canada	North America	Continent Comparison
1856	Canada	North America	Continent Comparison
1856	Canada	North America	Continent Comparison
1856	Canada	North America	Continent Comparison
1856	Canada	North America	Continent Comparison
1856	Canada	North America	Continent Comparison
1857	Canada	North America	Continent Comparison
1857	Canada	North America	Continent Comparison
1857	Canada	North America	Continent Comparison
1857	Canada	North America	Continent Comparison
1857	Canada	North America	Continent Comparison
1857	Canada	North America	Continent Comparison
1857	Canada	North America	Continent Comparison
1858	Canada	North America	Continent Comparison
1858	Canada	North America	Continent Comparison

1757	South Korea	Asia	100perContinent	1858	Canada	North America		Continent Comparison
1785	South Korea	Asia	100perContinent	1858	Canada	North America		Continent Comparison
1818	South Korea	Asia	100perContinent	1858	Canada	North America		Continent Comparison
1753	India	Asia	100perContinent	1858	Canada	North America		Continent Comparison
1755	Indonesia	Asia	100perContinent	1858	Canada	North America		Continent Comparison
1752	Indonesia	Asia	100perContinent	1858	Canada	North America		Continent Comparison
1743	Pakistan	Asia	100perContinent	1858	Canada	North America		Continent Comparison
1739	India	Asia	100perContinent	1859	Canada	North America		Continent Comparison
1746	Lebanon	Asia	100perContinent	1859	Canada	North America		Continent Comparison
1747	Lebanon	Asia	100perContinent	1780	Australia	Oceania		100perContinent
1747	Lebanon	Asia	100perContinent	1775	New Zealand	Oceania		100perContinent
1746	Lebanon	Asia	100perContinent	1792	Vanuatu	Oceania		100perContinent
1746	Lebanon	Asia	100perContinent	1775	Australia	Oceania		100perContinent
1746	Lebanon	Asia	100perContinent	1764	Australia	Oceania		100perContinent
1746	Lebanon	Asia	100perContinent	1751	Australia	Oceania		100perContinent
1746	Lebanon	Asia	100perContinent	1765	Australia	Oceania	New South Wales	NSW isolate
1747	Lebanon	Asia	100perContinent	1769	Australia	Oceania	New South Wales	NSW isolate
1746	Lebanon	Asia	100perContinent	1769	Australia	Oceania	New South Wales	NSW isolate
1747	Lebanon	Asia	100perContinent	1769	Australia	Oceania	New South Wales	NSW isolate

1746				1769					
0	Lebanon	Asia	100perContinent	3	Australia	Oceania	New South Wales	NSW isolate	
1747				1769					
6	Lebanon	Asia	100perContinent	4	Australia	Oceania	New South Wales	NSW isolate	
1748				1769					
8	Taiwan	Asia	100perContinent	5	Australia	Oceania	New South Wales	NSW isolate	
1748				1763					
7	Taiwan	Asia	100perContinent	0	Australia	Oceania	New South Wales	NSW isolate	
1749				1762					
2	Taiwan	Asia	100perContinent	1	Australia	Oceania	New South Wales	NSW isolate	
1748				1764					
3	Taiwan	Asia	100perContinent	2	Australia	Oceania	New South Wales	NSW isolate	
1748				1762					
5	Taiwan	Asia	100perContinent	2	Australia	Oceania	New South Wales	NSW isolate	
1749				1763					
3	Taiwan	Asia	100perContinent	2	Australia	Oceania	New South Wales	NSW isolate	
1749				1762					
5	Taiwan	Asia	100perContinent	9	Australia	Oceania	New South Wales	NSW isolate	
1748				1763					
6	Taiwan	Asia	100perContinent	1	Australia	Oceania	New South Wales	NSW isolate	
1748				1763					
1	Taiwan	Asia	100perContinent	5	Australia	Oceania	New South Wales	NSW isolate	
1737				1763					
5	Malaysia	Asia	100perContinent	4	Australia	Oceania	New South Wales	NSW isolate	
1751				1762					
2	Singapore	Asia	100perContinent	3	Australia	Oceania	New South Wales	NSW isolate	
1751				1762					
1	Singapore	Asia	100perContinent	8	Australia	Oceania	New South Wales	NSW isolate	
1751				1763					
0	Singapore	Asia	100perContinent	3	Australia	Oceania	New South Wales	NSW isolate	
1750				1763					
0	Singapore	Asia	100perContinent	6	Australia	Oceania	New South Wales	NSW isolate	
1750				1763					
9	Singapore	Asia	100perContinent	7	Australia	Oceania	New South Wales	NSW isolate	
1750				1763					
8	Singapore	Asia	100perContinent	8	Australia	Oceania	New South Wales	NSW isolate	
1750				1763					
7	Singapore	Asia	100perContinent	9	Australia	Oceania	New South Wales	NSW isolate	

1750 2	Singapore	Asia	100perContinent	1764 0	Australia	Oceania	New South Wales	NSW isolate
1750 4	Singapore	Asia	100perContinent	1764 3	Australia	Oceania	New South Wales	NSW isolate
1750 5	Singapore	Asia	100perContinent	1765 4	Australia	Oceania	New South Wales	NSW isolate
1751 4	Singapore	Asia	100perContinent	1765 3	Australia	Oceania	New South Wales	NSW isolate
1751 3	Singapore	Asia	100perContinent	1765 5	Australia	Oceania	New South Wales	NSW isolate
1751 5	Singapore	Asia	100perContinent	1765 6	Australia	Oceania	New South Wales	NSW isolate
1794 6	Israel	Asia	100perContinent	1764 4	Australia	Oceania	New South Wales	NSW isolate
1747 8	Jordan	Asia	100perContinent	1765 8	Australia	Oceania	New South Wales	NSW isolate
1747 9	Jordan	Asia	100perContinent	1765 7	Australia	Oceania	New South Wales	NSW isolate
1737 6	Malaysia	Asia	100perContinent	1764 5	Australia	Oceania	New South Wales	NSW isolate
1773 4	China	Asia	Continent Comparison	1765 9	Australia	Oceania	New South Wales	NSW isolate
1840 0	Taiwan	Asia	Continent Comparison	1766 3	Australia	Oceania	New South Wales	NSW isolate
1835 8	Taiwan	Asia	Continent Comparison	1766 0	Australia	Oceania	New South Wales	NSW isolate
1839 2	Taiwan	Asia	Continent Comparison	1764 6	Australia	Oceania	New South Wales	NSW isolate
1835 3	Taiwan	Asia	Continent Comparison	1766 1	Australia	Oceania	New South Wales	NSW isolate
1838 8	Taiwan	Asia	Continent Comparison	1766 2	Australia	Oceania	New South Wales	NSW isolate
1841 2	China	Asia	Continent Comparison	1764 7	Australia	Oceania	New South Wales	NSW isolate
1841 4	China	Asia	Continent Comparison	1767 5	Australia	Oceania	New South Wales	NSW isolate
1840 8	China	Asia	Continent Comparison	1767 4	Australia	Oceania	New South Wales	NSW isolate

1840				1766				
3	Taiwan	Asia	Continent Comparison	8	Australia	Oceania	New South Wales	NSW isolate
1842				1767				
0	Singapore	Asia	Continent Comparison	6	Australia	Oceania	New South Wales	NSW isolate
1842				1766				
3	Singapore	Asia	Continent Comparison	4	Australia	Oceania	New South Wales	NSW isolate
1836				1764				
5	Singapore	Asia	Continent Comparison	8	Australia	Oceania	New South Wales	NSW isolate
1831				1767				
4	Singapore	Asia	Continent Comparison	1	Australia	Oceania	New South Wales	NSW isolate
1834				1772				
0	Singapore	Asia	Continent Comparison	8	Australia	Oceania	New South Wales	NSW isolate
1737				1772				
9	China	Asia	Continent Comparison	1	Australia	Oceania	New South Wales	NSW isolate
1836				1772				
4	China	Asia	Continent Comparison	2	Australia	Oceania	New South Wales	NSW isolate
1742				1772				
5	China	Asia	Continent Comparison	3	Australia	Oceania	New South Wales	NSW isolate
1841				1767				
1	China	Asia	Continent Comparison	7	Australia	Oceania	New South Wales	NSW isolate
1840				1767				
7	China	Asia	Continent Comparison	9	Australia	Oceania	New South Wales	NSW isolate
1840				1767				
9	China	Asia	Continent Comparison	0	Australia	Oceania	New South Wales	NSW isolate
1739				1767				
4	China	Asia	Continent Comparison	8	Australia	Oceania	New South Wales	NSW isolate
1836				1768				
3	China	Asia	Continent Comparison	0	Australia	Oceania	New South Wales	NSW isolate
1839				1767				
0	Taiwan	Asia	Continent Comparison	2	Australia	Oceania	New South Wales	NSW isolate
1841				1768				
0	China	Asia	Continent Comparison	1	Australia	Oceania	New South Wales	NSW isolate
1841				1767				
3	China	Asia	Continent Comparison	3	Australia	Oceania	New South Wales	NSW isolate
1834				1766				
4	Taiwan	Asia	Continent Comparison	6	Australia	Oceania	New South Wales	NSW isolate
1836				1764				
1	China	Asia	Continent Comparison	9	Australia	Oceania	New South Wales	NSW isolate

1742				1765			New	
4	China	Asia	Continent Comparison	0	Australia	Oceania	South Wales	NSW isolate
1836				1766			New	
0	China	Asia	Continent Comparison	5	Australia	Oceania	South Wales	NSW isolate
1776				1765			New	
0	Taiwan	Asia	Continent Comparison	1	Australia	Oceania	South Wales	NSW isolate
1776				1768			New	
1	Taiwan	Asia	Continent Comparison	4	Australia	Oceania	South Wales	NSW isolate
1843				1768			New	
5	China	Asia	Continent Comparison	3	Australia	Oceania	South Wales	NSW isolate
1738				1768			New	
1	China	Asia	Continent Comparison	2	Australia	Oceania	South Wales	NSW isolate
1738				1768			New	
9	China	Asia	Continent Comparison	5	Australia	Oceania	South Wales	NSW isolate
1836				1768			New	
2	China	Asia	Continent Comparison	7	Australia	Oceania	South Wales	NSW isolate
1840				1768			New	
6	China	Asia	Continent Comparison	8	Australia	Oceania	South Wales	NSW isolate
1843				1768			New	
4	Taiwan	Asia	Continent Comparison	9	Australia	Oceania	South Wales	NSW isolate
1747				1769			New	
2	Lebanon	Asia	Continent Comparison	6	Australia	Oceania	South Wales	NSW isolate
1746				1769			New	
2	Lebanon	Asia	Continent Comparison	7	Australia	Oceania	South Wales	NSW isolate
1834				1769			New	
8	Taiwan	Asia	Continent Comparison	8	Australia	Oceania	South Wales	NSW isolate
1843				1769			New	
0	Taiwan	Asia	Continent Comparison	9	Australia	Oceania	South Wales	NSW isolate
1834				1770			New	
5	Taiwan	Asia	Continent Comparison	0	Australia	Oceania	South Wales	NSW isolate
1839				1770			New	
1	Taiwan	Asia	Continent Comparison	1	Australia	Oceania	South Wales	NSW isolate
1834				1770			New	
9	Taiwan	Asia	Continent Comparison	2	Australia	Oceania	South Wales	NSW isolate
1839				1770			New	
4	Taiwan	Asia	Continent Comparison	3	Australia	Oceania	South Wales	NSW isolate
1842				1770			New	
6	Taiwan	Asia	Continent Comparison	4	Australia	Oceania	South Wales	NSW isolate

1840404	Taiwan	Asia	Continent Comparison	1770705	Australia	Oceania	New South Wales	NSW isolate
1834402	Taiwan	Asia	Continent Comparison	1770706	Australia	Oceania	New South Wales	NSW isolate
1842409	Taiwan	Asia	Continent Comparison	1770707	Australia	Oceania	New South Wales	NSW isolate
1835404	Taiwan	Asia	Continent Comparison	1770708	Australia	Oceania	New South Wales	NSW isolate
1748402	Taiwan	Asia	Continent Comparison	1770709	Australia	Oceania	New South Wales	NSW isolate
1843401	Taiwan	Asia	Continent Comparison	1771000	Australia	Oceania	New South Wales	NSW isolate
1748404	Taiwan	Asia	Continent Comparison	1771001	Australia	Oceania	New South Wales	NSW isolate
1835400	Taiwan	Asia	Continent Comparison	1771002	Australia	Oceania	New South Wales	NSW isolate
1839409	Taiwan	Asia	Continent Comparison	1771004	Australia	Oceania	New South Wales	NSW isolate
1835407	Taiwan	Asia	Continent Comparison	1771005	Australia	Oceania	New South Wales	NSW isolate
1839403	Taiwan	Asia	Continent Comparison	1771006	Australia	Oceania	New South Wales	NSW isolate
1834406	Taiwan	Asia	Continent Comparison	1771007	Australia	Oceania	New South Wales	NSW isolate
1839407	Taiwan	Asia	Continent Comparison	1771008	Australia	Oceania	New South Wales	NSW isolate
1838406	Taiwan	Asia	Continent Comparison	1771009	Australia	Oceania	New South Wales	NSW isolate
1840402	Taiwan	Asia	Continent Comparison	1772000	Australia	Oceania	New South Wales	NSW isolate
1749404	Taiwan	Asia	Continent Comparison	1798704	Australia	Oceania	Queensland	Queensland Isolate
1842408	Taiwan	Asia	Continent Comparison	1798808	Australia	Oceania	Queensland	Queensland Isolate
1835401	Taiwan	Asia	Continent Comparison	1799606	Australia	Oceania	Queensland	Queensland Isolate
1748409	Taiwan	Asia	Continent Comparison	1799808	Australia	Oceania	Queensland	Queensland Isolate

1748				1799				
0	Taiwan	Asia	Continent Comparison	9	Australia	Oceania	Queensland	Queensland Isolate
1835				1800				
6	Taiwan	Asia	Continent Comparison	1	Australia	Oceania	Queensland	Queensland Isolate
1839				1800				
5	Taiwan	Asia	Continent Comparison	2	Australia	Oceania	Queensland	Queensland Isolate
1834				1800				
7	Taiwan	Asia	Continent Comparison	4	Australia	Oceania	Queensland	Queensland Isolate
1835				1800				
2	Taiwan	Asia	Continent Comparison	5	Australia	Oceania	Queensland	Queensland Isolate
1840				1800				
1	Taiwan	Asia	Continent Comparison	6	Australia	Oceania	Queensland	Queensland Isolate
1834				1800				
3	Taiwan	Asia	Continent Comparison	7	Australia	Oceania	Queensland	Queensland Isolate
1835				1801				
5	Taiwan	Asia	Continent Comparison	0	Australia	Oceania	Queensland	Queensland Isolate
1843				1801				
2	Taiwan	Asia	Continent Comparison	9	Australia	Oceania	Queensland	Queensland Isolate
1842				1802				
5	Taiwan	Asia	Continent Comparison	0	Australia	Oceania	Queensland	Queensland Isolate
1839				1802				
6	Taiwan	Asia	Continent Comparison	1	Australia	Oceania	Queensland	Queensland Isolate
1839				1802				
8	Taiwan	Asia	Continent Comparison	2	Australia	Oceania	Queensland	Queensland Isolate
1838				1802				
7	Taiwan	Asia	Continent Comparison	4	Australia	Oceania	Queensland	Queensland Isolate
1838				1802				
5	Taiwan	Asia	Continent Comparison	6	Australia	Oceania	Queensland	Queensland Isolate
1842				1802				
7	Taiwan	Asia	Continent Comparison	7	Australia	Oceania	Queensland	Queensland Isolate
1838				1802				
9	Taiwan	Asia	Continent Comparison	8	Australia	Oceania	Queensland	Queensland Isolate
1841				1803				
7	Singapore	Asia	Continent Comparison	0	Australia	Oceania	Queensland	Queensland Isolate
1833				1803				
7	Singapore	Asia	Continent Comparison	4	Australia	Oceania	Queensland	Queensland Isolate
1831				1803				
6	Singapore	Asia	Continent Comparison	7	Australia	Oceania	Queensland	Queensland Isolate

1837	Singapore	Asia	Continent Comparison	1803	Australia	Oceania	Queensland	Queensland Isolate
1838	Singapore	Asia	Continent Comparison	1803	Australia	Oceania	Queensland	Queensland Isolate
1837	Singapore	Asia	Continent Comparison	1804	Australia	Oceania	Queensland	Queensland Isolate
1841	Singapore	Asia	Continent Comparison	1804	Australia	Oceania	Queensland	Queensland Isolate
1749	Singapore	Asia	Continent Comparison	1804	Australia	Oceania	Queensland	Queensland Isolate
1749	Singapore	Asia	Continent Comparison	1805	Australia	Oceania	Queensland	Queensland Isolate
1837	Singapore	Asia	Continent Comparison	1805	Australia	Oceania	Queensland	Queensland Isolate
1832	Singapore	Asia	Continent Comparison	1805	Australia	Oceania	Queensland	Queensland Isolate
1841	Singapore	Asia	Continent Comparison	1805	Australia	Oceania	Queensland	Queensland Isolate
1831	Singapore	Asia	Continent Comparison	1806	Australia	Oceania	Queensland	Queensland Isolate
1832	Singapore	Asia	Continent Comparison	1806	Australia	Oceania	Queensland	Queensland Isolate
1842	Singapore	Asia	Continent Comparison	1806	Australia	Oceania	Queensland	Queensland Isolate
1832	Singapore	Asia	Continent Comparison	1807	Australia	Oceania	Queensland	Queensland Isolate
1831	Singapore	Asia	Continent Comparison	1807	Australia	Oceania	Queensland	Queensland Isolate
1833	Singapore	Asia	Continent Comparison	1807	Australia	Oceania	Queensland	Queensland Isolate
1832	Singapore	Asia	Continent Comparison	1807	Australia	Oceania	Queensland	Queensland Isolate
1831	Singapore	Asia	Continent Comparison	1807	Australia	Oceania	Queensland	Queensland Isolate
1750	Singapore	Asia	Continent Comparison	1807	Australia	Oceania	Queensland	Queensland Isolate
1831	Singapore	Asia	Continent Comparison	1807	Australia	Oceania	Queensland	Queensland Isolate

1836	Singapore	Asia	Continent Comparison	1808	Australia	Oceania	Queensland	Queensland Isolate
1833	Singapore	Asia	Continent Comparison	1817	Australia	Oceania	Queensland	Queensland Isolate
1750	Singapore	Asia	Continent Comparison	1808	Australia	Oceania	Queensland	Queensland Isolate
1833	Singapore	Asia	Continent Comparison	1808	Australia	Oceania	Queensland	Queensland Isolate
1837	Singapore	Asia	Continent Comparison	1808	Australia	Oceania	Queensland	Queensland Isolate
1833	Singapore	Asia	Continent Comparison	1808	Australia	Oceania	Queensland	Queensland Isolate
1841	Singapore	Asia	Continent Comparison	1808	Australia	Oceania	Queensland	Queensland Isolate
1841	Singapore	Asia	Continent Comparison	1809	Australia	Oceania	Queensland	Queensland Isolate
1831	Singapore	Asia	Continent Comparison	1809	Australia	Oceania	Queensland	Queensland Isolate
1832	Singapore	Asia	Continent Comparison	1810	Australia	Oceania	Queensland	Queensland Isolate
1836	Singapore	Asia	Continent Comparison	1810	Australia	Oceania	Queensland	Queensland Isolate
1834	Singapore	Asia	Continent Comparison	1810	Australia	Oceania	Queensland	Queensland Isolate
1833	Singapore	Asia	Continent Comparison	1810	Australia	Oceania	Queensland	Queensland Isolate
1838	Singapore	Asia	Continent Comparison	1810	Australia	Oceania	Queensland	Queensland Isolate
1836	Singapore	Asia	Continent Comparison	1810	Australia	Oceania	Queensland	Queensland Isolate
1833	Singapore	Asia	Continent Comparison	1811	Australia	Oceania	Queensland	Queensland Isolate
1833	Singapore	Asia	Continent Comparison	1811	Australia	Oceania	Queensland	Queensland Isolate
1838	Singapore	Asia	Continent Comparison	1811	Australia	Oceania	Queensland	Queensland Isolate
1832	Singapore	Asia	Continent Comparison	1812	Australia	Oceania	Queensland	Queensland Isolate

1837	Singapore	Asia	Continent Comparison	1812	Australia	Oceania	Queensland	Queensland Isolate
1837	Singapore	Asia	Continent Comparison	1812	Australia	Oceania	Queensland	Queensland Isolate
1837	Singapore	Asia	Continent Comparison	1813	Australia	Oceania	Queensland	Queensland Isolate
1837	Singapore	Asia	Continent Comparison	1813	Australia	Oceania	Queensland	Queensland Isolate
1838	Singapore	Asia	Continent Comparison	1813	Australia	Oceania	Queensland	Queensland Isolate
1751	Singapore	Asia	Continent Comparison	1813	Australia	Oceania	Queensland	Queensland Isolate
1836	Singapore	Asia	Continent Comparison	1813	Australia	Oceania	Queensland	Queensland Isolate
1842	Singapore	Asia	Continent Comparison	1813	Australia	Oceania	Queensland	Queensland Isolate
1837	Singapore	Asia	Continent Comparison	1813	Australia	Oceania	Queensland	Queensland Isolate
1842	Singapore	Asia	Continent Comparison	1814	Australia	Oceania	Queensland	Queensland Isolate
1832	Singapore	Asia	Continent Comparison	1814	Australia	Oceania	Queensland	Queensland Isolate
1833	Singapore	Asia	Continent Comparison	1814	Australia	Oceania	Queensland	Queensland Isolate
1832	Singapore	Asia	Continent Comparison	1814	Australia	Oceania	Queensland	Queensland Isolate
1837	Singapore	Asia	Continent Comparison	1814	Australia	Oceania	Queensland	Queensland Isolate
1832	Singapore	Asia	Continent Comparison	1815	Australia	Oceania	Queensland	Queensland Isolate
1750	Singapore	Asia	Continent Comparison	1815	Australia	Oceania	Queensland	Queensland Isolate
1838	Singapore	Asia	Continent Comparison	1815	Australia	Oceania	Queensland	Queensland Isolate
1833	Singapore	Asia	Continent Comparison	1815	Australia	Oceania	Queensland	Queensland Isolate
1832	Singapore	Asia	Continent Comparison	1815	Australia	Oceania	Queensland	Queensland Isolate

1751				1816				
6	Singapore	Asia	Continent Comparison	1	Australia	Oceania	Queensland	Queensland Isolate
1835				1816				
9	China	Asia	Continent Comparison	2	Australia	Oceania	Queensland	Queensland Isolate
1840				1816				
5	China	Asia	Continent Comparison	3	Australia	Oceania	Queensland	Queensland Isolate
1760				1816				
8	Germany	Europe	100perContinent	4	Australia	Oceania	Queensland	Queensland Isolate
1737				1816				
7	Sweden	Europe	100perContinent	7	Australia	Oceania	Queensland	Queensland Isolate
1761				1816				
1	Austria	Europe	100perContinent	8	Australia	Oceania	Queensland	Queensland Isolate
1761				1817				
3	Austria	Europe	100perContinent	0	Australia	Oceania	Queensland	Queensland Isolate
1761				1817				
4	Austria	Europe	100perContinent	4	Australia	Oceania	Queensland	Queensland Isolate
1761				1817				
5	Austria	Europe	100perContinent	5	Australia	Oceania	Queensland	Queensland Isolate
1761				1817				
6	Austria	Europe	100perContinent	6	Australia	Oceania	Queensland	Queensland Isolate
1761				1817				
7	Germany	Europe	100perContinent	7	Australia	Oceania	Queensland	Queensland Isolate
1739				1798				
3	UK	Europe	100perContinent	5	Australia	Oceania	Queensland	Queensland Isolate100
1786				1798				
6	Finland	Europe	100perContinent	6	Australia	Oceania	Queensland	Queensland Isolate100
1758				1798				
7	Finland	Europe	100perContinent	9	Australia	Oceania	Queensland	Queensland Isolate100
1787				1799				
9	UK	Europe	100perContinent	0	Australia	Oceania	Queensland	Queensland Isolate100
1787				1799				
7	UK	Europe	100perContinent	1	Australia	Oceania	Queensland	Queensland Isolate100
1792				1799				
7	Spain	Europe	100perContinent	2	Australia	Oceania	Queensland	Queensland Isolate100
1792				1799				
8	Spain	Europe	100perContinent	3	Australia	Oceania	Queensland	Queensland Isolate100
1792				1799				
5	Spain	Europe	100perContinent	7	Australia	Oceania	Queensland	Queensland Isolate100

17926	Spain	Europe	100perContinent	18000	Australia	Oceania	Queensland	QueenslandIsolate100
17876	UK	Europe	100perContinent	18003	Australia	Oceania	Queensland	QueenslandIsolate100
17883	UK	Europe	100perContinent	18008	Australia	Oceania	Queensland	QueenslandIsolate100
17882	UK	Europe	100perContinent	18009	Australia	Oceania	Queensland	QueenslandIsolate100
18181	Greece	Europe	100perContinent	18011	Australia	Oceania	Queensland	QueenslandIsolate100
17963	Luxembourg	Europe	100perContinent	18012	Australia	Oceania	Queensland	QueenslandIsolate100
17965	Luxembourg	Europe	100perContinent	18013	Australia	Oceania	Queensland	QueenslandIsolate100
17834	Luxembourg	Europe	100perContinent	18014	Australia	Oceania	Queensland	QueenslandIsolate100
17966	Luxembourg	Europe	100perContinent	18015	Australia	Oceania	Queensland	QueenslandIsolate100
17975	Luxembourg	Europe	100perContinent	18016	Australia	Oceania	Queensland	QueenslandIsolate100
17584	The Netherlands	Europe	100perContinent	18017	Australia	Oceania	Queensland	QueenslandIsolate100
17586	The Netherlands	Europe	100perContinent	18018	Australia	Oceania	Queensland	QueenslandIsolate100
17775	The Netherlands	Europe	100perContinent	18023	Australia	Oceania	Queensland	QueenslandIsolate100
17772	The Netherlands	Europe	100perContinent	18025	Australia	Oceania	Queensland	QueenslandIsolate100
17771	The Netherlands	Europe	100perContinent	18029	Australia	Oceania	Queensland	QueenslandIsolate100
17782	The Netherlands	Europe	100perContinent	18031	Australia	Oceania	Queensland	QueenslandIsolate100
17808	The Netherlands	Europe	100perContinent	18032	Australia	Oceania	Queensland	QueenslandIsolate100
17620	Slovenia	Europe	100perContinent	18033	Australia	Oceania	Queensland	QueenslandIsolate100
17626	Slovenia	Europe	100perContinent	18035	Australia	Oceania	Queensland	QueenslandIsolate100

1743	Denmark	Europe	100perContinent	1803	Australia	Oceania	Queensland	QueenslandIsolate100
1745	Denmark	Europe	100perContinent	1804	Australia	Oceania	Queensland	QueenslandIsolate100
1819	Poland	Europe	100perContinent	1804	Australia	Oceania	Queensland	QueenslandIsolate100
1821	Italy	Europe	100perContinent	1804	Australia	Oceania	Queensland	QueenslandIsolate100
1821	Italy	Europe	100perContinent	1804	Australia	Oceania	Queensland	QueenslandIsolate100
1820	Italy	Europe	100perContinent	1804	Australia	Oceania	Queensland	QueenslandIsolate100
1820	Italy	Europe	100perContinent	1804	Australia	Oceania	Queensland	QueenslandIsolate100
1821	Italy	Europe	100perContinent	1804	Australia	Oceania	Queensland	QueenslandIsolate100
1821	Italy	Europe	100perContinent	1805	Australia	Oceania	Queensland	QueenslandIsolate100
1791	Norway	Europe	100perContinent	1805	Australia	Oceania	Queensland	QueenslandIsolate100
1780	Norway	Europe	100perContinent	1805	Australia	Oceania	Queensland	QueenslandIsolate100
1780	Norway	Europe	100perContinent	1805	Australia	Oceania	Queensland	QueenslandIsolate100
1780	Norway	Europe	100perContinent	1805	Australia	Oceania	Queensland	QueenslandIsolate100
1792	Norway	Europe	100perContinent	1805	Australia	Oceania	Queensland	QueenslandIsolate100
1744	Denmark	Europe	100perContinent	1806	Australia	Oceania	Queensland	QueenslandIsolate100
1745	Denmark	Europe	100perContinent	1806	Australia	Oceania	Queensland	QueenslandIsolate100
1744	Denmark	Europe	100perContinent	1806	Australia	Oceania	Queensland	QueenslandIsolate100
1744	Denmark	Europe	100perContinent	1806	Australia	Oceania	Queensland	QueenslandIsolate100
1779	Norway	Europe	100perContinent	1806	Australia	Oceania	Queensland	QueenslandIsolate100

1784	Norway	Europe	100perContinent	1806	Australia	Oceania	Queensland	Queensland Isolate100
1797	Luxembourg	Europe	100perContinent	1806	Australia	Oceania	Queensland	Queensland Isolate100
1797	Luxembourg	Europe	100perContinent	1807	Australia	Oceania	Queensland	Queensland Isolate100
1741	Belgium	Europe	100perContinent	1807	Australia	Oceania	Queensland	Queensland Isolate100
1741	Belgium	Europe	100perContinent	1808	Australia	Oceania	Queensland	Queensland Isolate100
1741	Belgium	Europe	100perContinent	1808	Australia	Oceania	Queensland	Queensland Isolate100
1740	Belgium	Europe	100perContinent	1808	Australia	Oceania	Queensland	Queensland Isolate100
1783	Austria	Europe	100perContinent	1808	Australia	Oceania	Queensland	Queensland Isolate100
1783	Czech Republic	Europe	100perContinent	1809	Australia	Oceania	Queensland	Queensland Isolate100
1784	Italy	Europe	100perContinent	1809	Australia	Oceania	Queensland	Queensland Isolate100
1784	Portugal	Europe	100perContinent	1809	Australia	Oceania	Queensland	Queensland Isolate100
1784	Romania	Europe	100perContinent	1809	Australia	Oceania	Queensland	Queensland Isolate100
1784	Spain	Europe	100perContinent	1809	Australia	Oceania	Queensland	Queensland Isolate100
1784	Hungary	Europe	100perContinent	1809	Australia	Oceania	Queensland	Queensland Isolate100
1784	Hungary	Europe	100perContinent	1809	Australia	Oceania	Queensland	Queensland Isolate100
1784	Portugal	Europe	100perContinent	1809	Australia	Oceania	Queensland	Queensland Isolate100
1784	Hungary	Europe	100perContinent	1810	Australia	Oceania	Queensland	Queensland Isolate100
1818	Germany	Europe	100perContinent	1810	Australia	Oceania	Queensland	Queensland Isolate100
1740	Hungary	Europe	100perContinent	1810	Australia	Oceania	Queensland	Queensland Isolate100

1752	Lithuania	Europe	100perContinent	1810	Australia	Oceania	Queensland	Queensland Isolate100
1790	Ireland	Europe	100perContinent	1811	Australia	Oceania	Queensland	Queensland Isolate100
1787	Ireland	Europe	100perContinent	1811	Australia	Oceania	Queensland	Queensland Isolate100
1788	Ireland	Europe	100perContinent	1811	Australia	Oceania	Queensland	Queensland Isolate100
1788	Ireland	Europe	100perContinent	1811	Australia	Oceania	Queensland	Queensland Isolate100
1819	Ireland	Europe	100perContinent	1811	Australia	Oceania	Queensland	Queensland Isolate100
1724	Germany	Europe	100perContinent	1812	Australia	Oceania	Queensland	Queensland Isolate100
1581	UK	Europe	100perContinent	1812	Australia	Oceania	Queensland	Queensland Isolate100
1822	Poland	Europe	100perContinent	1812	Australia	Oceania	Queensland	Queensland Isolate100
1822	Poland	Europe	100perContinent	1812	Australia	Oceania	Queensland	Queensland Isolate100
1822	Poland	Europe	100perContinent	1812	Australia	Oceania	Queensland	Queensland Isolate100
1819	Poland	Europe	100perContinent	1812	Australia	Oceania	Queensland	Queensland Isolate100
1788	Belgium	Europe	100perContinent	1812	Australia	Oceania	Queensland	Queensland Isolate100
1790	Belgium	Europe	100perContinent	1813	Australia	Oceania	Queensland	Queensland Isolate100
1792	Sweden	Europe	100perContinent	1813	Australia	Oceania	Queensland	Queensland Isolate100
1793	Sweden	Europe	100perContinent	1813	Australia	Oceania	Queensland	Queensland Isolate100
1794	Sweden	Europe	100perContinent	1814	Australia	Oceania	Queensland	Queensland Isolate100
1795	Sweden	Europe	100perContinent	1814	Australia	Oceania	Queensland	Queensland Isolate100
1797	Sweden	Europe	100perContinent	1814	Australia	Oceania	Queensland	Queensland Isolate100

1791	Germany	Europe	100perContinent
1791	Germany	Europe	100perContinent
1818	Poland	Europe	100perContinent
1819	Poland	Europe	100perContinent
1745	Ireland	Europe	100perContinent
1754	Switzerland	Europe	100perContinent
1772	Germany	Europe	100perContinent
1782	Ireland	Europe	100perContinent
1760	Germany	Europe	Continent Comparison
1760	Germany	Europe	Continent Comparison
1761	Germany	Europe	Continent Comparison
1761	Austria	Europe	Continent Comparison
1754	UK	Europe	Continent Comparison
1755	UK	Europe	Continent Comparison
1761	Germany	Europe	Continent Comparison
1761	Germany	Europe	Continent Comparison
1754	UK	Europe	Continent Comparison
1823	UK	Europe	Continent Comparison
1788	UK	Europe	Continent Comparison
1814	Australia	Oceania	Queensland	Queensland Isolate100
1815	Australia	Oceania	Queensland	Queensland Isolate100
1815	Australia	Oceania	Queensland	Queensland Isolate100
1815	Australia	Oceania	Queensland	Queensland Isolate100
1815	Australia	Oceania	Queensland	Queensland Isolate100
1815	Australia	Oceania	Queensland	Queensland Isolate100
1816	Australia	Oceania	Queensland	Queensland Isolate100
1816	Australia	Oceania	Queensland	Queensland Isolate100
1816	Australia	Oceania	Queensland	Queensland Isolate100
1816	Australia	Oceania	Queensland	Queensland Isolate100
1817	Australia	Oceania	Queensland	Queensland Isolate100
1817	Australia	Oceania	Queensland	Queensland Isolate100
1817	Australia	Oceania	Queensland	Queensland Isolate100
1817	Australia	Oceania	Queensland	Queensland Isolate100
1795	Uruguay	South America		100perContinent
1794	Uruguay	South America		100perContinent
1795	Uruguay	South America		100perContinent

1788	UK	Europe	Continent Comparison	1795	Uruguay	South America	100perContinent
1794	UK	Europe	Continent Comparison	1794	Uruguay	South America	100perContinent
1747	UK	Europe	Continent Comparison	1795	Uruguay	South America	100perContinent
1740	UK	Europe	Continent Comparison	1795	Uruguay	South America	100perContinent
1752	UK	Europe	Continent Comparison	1818	Uruguay	South America	100perContinent
1753	UK	Europe	Continent Comparison	1794	Uruguay	South America	100perContinent
1796	Luxembourg	Europe	Continent Comparison	1806	Argentina	South America	100perContinent
1796	Luxembourg	Europe	Continent Comparison	1856	Argentina	South America	100perContinent
1797	Luxembourg	Europe	Continent Comparison	1730	Argentina	South America	100perContinent
1798	Luxembourg	Europe	Continent Comparison	1805	Argentina	South America	100perContinent
1759	The Netherlands	Europe	Continent Comparison	1832	Argentina	South America	100perContinent
1758	The Netherlands	Europe	Continent Comparison	1831	Argentina	South America	100perContinent
1759	The Netherlands	Europe	Continent Comparison	1823	Chile	South America	100perContinent
1776	The Netherlands	Europe	Continent Comparison	1831	Chile	South America	100perContinent
1777	The Netherlands	Europe	Continent Comparison	1830	Chile	South America	100perContinent
1778	The Netherlands	Europe	Continent Comparison	1753	Chile	South America	100perContinent
1779	The Netherlands	Europe	Continent Comparison	1753	Chile	South America	100perContinent
1780	The Netherlands	Europe	Continent Comparison	1823	Chile	South America	100perContinent
1781	The Netherlands	Europe	Continent Comparison	1831	Chile	South America	100perContinent

1770	The Netherlands	Europe	Continent Comparison	1823	Chile	South America	100perContinent
1785	The Netherlands	Europe	Continent Comparison	1830	Chile	South America	100perContinent
1814	The Netherlands	Europe	Continent Comparison	1753	Chile	South America	100perContinent
1809	The Netherlands	Europe	Continent Comparison	1843	Chile	South America	100perContinent
1741	Germany	Europe	Continent Comparison	1823	Chile	South America	100perContinent
1745	Denmark	Europe	Continent Comparison	1829	Chile	South America	100perContinent
1748	Denmark	Europe	Continent Comparison	1753	Chile	South America	100perContinent
1745	Denmark	Europe	Continent Comparison	1830	Chile	South America	100perContinent
1740	Denmark	Europe	Continent Comparison	1753	Chile	South America	100perContinent
1745	Denmark	Europe	Continent Comparison	1739	Argentina	South America	100perContinent
1745	Denmark	Europe	Continent Comparison	1739	Argentina	South America	100perContinent
1821	Italy	Europe	Continent Comparison	1739	Argentina	South America	100perContinent
1821	Italy	Europe	Continent Comparison	1739	Argentina	South America	100perContinent
1821	Italy	Europe	Continent Comparison	1739	Argentina	South America	100perContinent
1821	Italy	Europe	Continent Comparison	1754	Argentina	South America	100perContinent
1821	Italy	Europe	Continent Comparison	1759	Chile	South America	100perContinent
1820	Italy	Europe	Continent Comparison	1829	Chile	South America	100perContinent
1820	Italy	Europe	Continent Comparison	1759	Chile	South America	100perContinent
1821	Italy	Europe	Continent Comparison	1759	Chile	South America	100perContinent

1820				1843			
3	Italy	Europe	Continent Comparison	9	Chile	South America	100perContinent
1820				1829			
7	Italy	Europe	Continent Comparison	5	Chile	South America	100perContinent
1820				1829			
8	Italy	Europe	Continent Comparison	7	Chile	South America	100perContinent
1820				1823			
2	Italy	Europe	Continent Comparison	4	Chile	South America	100perContinent
1820				1759			
1	Italy	Europe	Continent Comparison	5	Chile	South America	100perContinent
1791				1759			
5	Norway	Europe	Continent Comparison	6	Chile	South America	100perContinent
1777				1759			
4	Norway	Europe	Continent Comparison	8	Chile	South America	100perContinent
1777				1759			
3	Norway	Europe	Continent Comparison	7	Chile	South America	100perContinent
1780				1759			
2	Norway	Europe	Continent Comparison	9	Chile	South America	100perContinent
1780				1829			
0	Norway	Europe	Continent Comparison	6	Chile	South America	100perContinent
1779				1831			
9	Norway	Europe	Continent Comparison	1	Chile	South America	100perContinent
1778				1760			
3	Norway	Europe	Continent Comparison	0	Chile	South America	100perContinent
1791				1830			
6	Norway	Europe	Continent Comparison	4	Chile	South America	100perContinent
1791				1775			
7	Norway	Europe	Continent Comparison	7	Peru	South America	100perContinent
1791				1775			
8	Norway	Europe	Continent Comparison	8	Peru	South America	100perContinent
1791				1752			
9	Norway	Europe	Continent Comparison	5	Chile	South America	100perContinent
1792				1785			
0	Norway	Europe	Continent Comparison	3	Brazil	South America	100perContinent
1792				1785			
2	Norway	Europe	Continent Comparison	4	Brazil	South America	100perContinent
1745				1824			
6	Denmark	Europe	Continent Comparison	3	Brazil	South America	100perContinent

1745	Denmark	Europe	Continent Comparison	1785	Brazil	South America	100perContinent
1744	Denmark	Europe	Continent Comparison	1829	Brazil	South America	100perContinent
1744	Denmark	Europe	Continent Comparison	1829	Brazil	South America	100perContinent
1745	Denmark	Europe	Continent Comparison	1785	Brazil	South America	100perContinent
1744	Denmark	Europe	Continent Comparison	1830	Brazil	South America	100perContinent
1744	Denmark	Europe	Continent Comparison	1828	Brazil	South America	100perContinent
1744	Denmark	Europe	Continent Comparison	1785	Brazil	South America	100perContinent
1823	UK	Europe	Continent Comparison	1828	Brazil	South America	100perContinent
1796	Luxembourg	Europe	Continent Comparison	1830	Brazil	South America	100perContinent
1797	Luxembourg	Europe	Continent Comparison	1785	Brazil	South America	100perContinent
1797	Luxembourg	Europe	Continent Comparison	1787	Brazil	South America	100perContinent
1797	Luxembourg	Europe	Continent Comparison	1787	Brazil	South America	100perContinent
1797	Luxembourg	Europe	Continent Comparison	1787	Brazil	South America	100perContinent
1797	Luxembourg	Europe	Continent Comparison	1787	Brazil	South America	100perContinent
1796	Luxembourg	Europe	Continent Comparison	1787	Brazil	South America	100perContinent
1796	Luxembourg	Europe	Continent Comparison	1789	Brazil	South America	100perContinent
1776	Luxembourg	Europe	Continent Comparison	1789	Brazil	South America	100perContinent
1753	Belgium	Europe	Continent Comparison	1786	Brazil	South America	100perContinent
1742	Belgium	Europe	Continent Comparison	1829	Brazil	South America	100perContinent

1753 7	Belgium	Europe	Continent Comparison	1787 0	Brazil	South America	100perContinent
1740 1	Belgium	Europe	Continent Comparison	1830 0	Brazil	South America	100perContinent
1741 6	Belgium	Europe	Continent Comparison	1830 2	Brazil	South America	100perContinent
1818 4	Germany	Europe	Continent Comparison	1830 7	Brazil	South America	100perContinent
1790 3	Ireland	Europe	Continent Comparison	1829 2	Brazil	South America	100perContinent
1762 5	Ireland	Europe	Continent Comparison	1786 7	Brazil	South America	100perContinent
1788 5	Ireland	Europe	Continent Comparison	1786 8	Brazil	South America	100perContinent
1788 4	Ireland	Europe	Continent Comparison	1786 3	Brazil	South America	100perContinent
1789 5	Ireland	Europe	Continent Comparison	1786 6	Brazil	South America	100perContinent
1789 4	Ireland	Europe	Continent Comparison	1742 2	Ecuador	South America	100perContinent
1819 3	Ireland	Europe	Continent Comparison	1762 4	Peru	South America	100perContinent
1795 6	Ireland	Europe	Continent Comparison	1743 3	Peru	South America	100perContinent
1798 4	Ireland	Europe	Continent Comparison	1743 5	Peru	South America	100perContinent
1822 9	Ireland	Europe	Continent Comparison	1743 6	Peru	South America	100perContinent
1768 6	Germany	Europe	Continent Comparison	1743 7	Peru	South America	100perContinent
1772 5	Germany	Europe	Continent Comparison	1743 4	Peru	South America	100perContinent
1772 7	Germany	Europe	Continent Comparison	1743 8	Peru	South America	100perContinent
1796 1	Germany	Europe	Continent Comparison	1829 0	Brazil	South America	100perContinent
1739 1	Belgium	Europe	Continent Comparison	1830 8	Brazil	South America	100perContinent

1822			Continent	1844		South	100perContinent
0	Poland	Europe	Comparison	0	Brazil	America	
1822			Continent	1844		South	100perContinent
1	Poland	Europe	Comparison	1	Brazil	America	
1822			Continent	1849		South	Continent
3	Poland	Europe	Comparison	2	Chile	America	Comparison
1822			Continent	1851		South	Continent
2	Poland	Europe	Comparison	8	Chile	America	Comparison
1819			Continent	1849		South	Continent
8	Poland	Europe	Comparison	7	Chile	America	Comparison
1819			Continent	1852		South	Continent
7	Poland	Europe	Comparison	1	Chile	America	Comparison
1819			Continent	1850		South	Continent
6	Poland	Europe	Comparison	1	Chile	America	Comparison
1819			Continent	1851		South	Continent
5	Poland	Europe	Comparison	4	Chile	America	Comparison
1778			Continent	1849		South	Continent
7	Belgium	Europe	Comparison	0	Chile	America	Comparison
1778			Continent	1851		South	Continent
9	Belgium	Europe	Comparison	9	Chile	America	Comparison
1779			Continent	1850		South	Continent
1	Belgium	Europe	Comparison	9	Chile	America	Comparison
1779			Continent	1849		South	Continent
6	Sweden	Europe	Comparison	4	Chile	America	Comparison
1791			Continent	1850		South	Continent
1	Germany	Europe	Comparison	0	Chile	America	Comparison
1792			Continent	1850		South	Continent
3	Germany	Europe	Comparison	3	Chile	America	Comparison
1818			Continent	1849		South	Continent
6	Poland	Europe	Comparison	8	Chile	America	Comparison
1818			Continent	1851		South	Continent
8	Poland	Europe	Comparison	1	Chile	America	Comparison
1818			Continent	1851		South	Continent
9	Poland	Europe	Comparison	7	Chile	America	Comparison
1819			Continent	1851		South	Continent
1	Poland	Europe	Comparison	2	Chile	America	Comparison
1818			Continent	1849		South	Continent
5	Poland	Europe	Comparison	1	Chile	America	Comparison

1749	Ireland	Europe	Continent Comparison	1851	Chile	South America	Continent Comparison
1784	UK	Europe	Continent Comparison	1849	Chile	South America	Continent Comparison
1782	Ireland	Europe	Continent Comparison	1852	Chile	South America	Continent Comparison
1782	Ireland	Europe	Continent Comparison	1850	Chile	South America	Continent Comparison
1786	Mexico	North America	100perContinent	1849	Chile	South America	Continent Comparison
1825	Canada	North America	100perContinent	1850	Chile	South America	Continent Comparison
1741	USA	North America	100perContinent	1850	Chile	South America	Continent Comparison
1828	USA	North America	100perContinent	1852	Chile	South America	Continent Comparison
1828	USA	North America	100perContinent	1851	Chile	South America	Continent Comparison
1824	Mexico	North America	100perContinent	1851	Chile	South America	Continent Comparison
1827	USA	North America	100perContinent	1850	Chile	South America	Continent Comparison
1783	USA	North America	100perContinent	1848	Chile	South America	Continent Comparison
1794	Mexico	North America	100perContinent	1849	Chile	South America	Continent Comparison
1825	Mexico	North America	100perContinent	1849	Chile	South America	Continent Comparison
1794	Mexico	North America	100perContinent	1850	Chile	South America	Continent Comparison
1825	Mexico	North America	100perContinent	1851	Chile	South America	Continent Comparison
1793	Mexico	North America	100perContinent	1850	Chile	South America	Continent Comparison
1825	Mexico	North America	100perContinent	1848	Brazil	South America	Continent Comparison
1793	Mexico	North America	100perContinent	1847	Brazil	South America	Continent Comparison

1793	Mexico	North America	100perContinent	1848	Brazil	South America	Continent Comparison
1794	Mexico	North America	100perContinent	1845	Brazil	South America	Continent Comparison
1793	Mexico	North America	100perContinent	1846	Brazil	South America	Continent Comparison
1794	Mexico	North America	100perContinent	1846	Brazil	South America	Continent Comparison
1793	Mexico	North America	100perContinent	1853	Brazil	South America	Continent Comparison
1793	Mexico	North America	100perContinent	1852	Brazil	South America	Continent Comparison
1793	Mexico	North America	100perContinent	1853	Brazil	South America	Continent Comparison
1793	Mexico	North America	100perContinent	1853	Brazil	South America	Continent Comparison
1795	Mexico	North America	100perContinent	1844	Brazil	South America	Continent Comparison
1824	Mexico	North America	100perContinent	1853	Brazil	South America	Continent Comparison
1794	Mexico	North America	100perContinent	1846	Brazil	South America	Continent Comparison
1795	Mexico	North America	100perContinent	1846	Brazil	South America	Continent Comparison
1828	USA	North America	100perContinent	1852	Brazil	South America	Continent Comparison
1762	USA	North America	100perContinent	1844	Brazil	South America	Continent Comparison
1826	Canada	North America	100perContinent	1854	Brazil	South America	Continent Comparison
1757	Canada	North America	100perContinent	1852	Brazil	South America	Continent Comparison
1826	Canada	North America	100perContinent	1853	Brazil	South America	Continent Comparison
1785	Canada	North America	100perContinent	1853	Brazil	South America	Continent Comparison
1786	Canada	North America	100perContinent	1853	Brazil	South America	Continent Comparison

18231	Mexico	North America	100perContinent	18454	Brazil	South America	Continent Comparison
17526	Mexico	North America	100perContinent	18445	Brazil	South America	Continent Comparison
17553	Mexico	North America	100perContinent	18480	Brazil	South America	Continent Comparison
17552	Mexico	North America	100perContinent	18529	Brazil	South America	Continent Comparison
17762	Dominican Republic	North America	100perContinent	18487	Brazil	South America	Continent Comparison
17763	Dominican Republic	North America	100perContinent	18473	Brazil	South America	Continent Comparison
17764	Dominican Republic	North America	100perContinent	18467	Brazil	South America	Continent Comparison
18271	USA	North America	100perContinent	18451	Brazil	South America	Continent Comparison
17523	Dominican Republic	North America	100perContinent	18537	Brazil	South America	Continent Comparison
18272	USA	North America	100perContinent	18476	Brazil	South America	Continent Comparison
18275	USA	North America	100perContinent	18450	Brazil	South America	Continent Comparison
18279	USA	North America	100perContinent	18523	Brazil	South America	Continent Comparison
18284	USA	North America	100perContinent	18466	Brazil	South America	Continent Comparison
17556	USA	North America	100perContinent	18456	Brazil	South America	Continent Comparison
18239	USA	North America	100perContinent	18485	Brazil	South America	Continent Comparison
18262	Canada	North America	100perContinent	18448	Brazil	South America	Continent Comparison
17519	USA	North America	100perContinent	18464	Brazil	South America	Continent Comparison
18280	USA	North America	100perContinent	18458	Brazil	South America	Continent Comparison
17527	USA	North America	100perContinent	18468	Brazil	South America	Continent Comparison

1773	USA	North America	100perContinent	1846	Brazil	South America	Continent Comparison
1827	USA	North America	100perContinent	1847	Brazil	South America	Continent Comparison
1827	USA	North America	100perContinent	1849	Brazil	South America	Continent Comparison
1828	USA	North America	100perContinent	1847	Brazil	South America	Continent Comparison
1789	USA	North America	100perContinent	1852	Brazil	South America	Continent Comparison
1828	USA	North America	100perContinent	1845	Brazil	South America	Continent Comparison
1792	USA	North America	100perContinent	1845	Brazil	South America	Continent Comparison
1828	USA	North America	100perContinent	1847	Brazil	South America	Continent Comparison
1793	USA	North America	100perContinent	1847	Brazil	South America	Continent Comparison
1827	USA	North America	100perContinent	1848	Brazil	South America	Continent Comparison
1793	USA	North America	100perContinent	1848	Brazil	South America	Continent Comparison
1824	USA	North America	100perContinent	1847	Brazil	South America	Continent Comparison
1795	USA	North America	100perContinent	1848	Brazil	South America	Continent Comparison
1796	USA	North America	100perContinent	1847	Brazil	South America	Continent Comparison
1827	USA	North America	100perContinent	1846	Brazil	South America	Continent Comparison
1798	USA	North America	100perContinent	1853	Brazil	South America	Continent Comparison
1824	USA	North America	100perContinent	1848	Brazil	South America	Continent Comparison
1798	USA	North America	100perContinent	1844	Brazil	South America	Continent Comparison
1826	Canada	North America	100perContinent	1853	Brazil	South America	Continent Comparison

1826264	Canada	North America	100perContinent	1852644	Brazil	South America	Continent Comparison
1825616	Canada	North America	100perContinent	1854161	Brazil	South America	Continent Comparison
1785848	Canada	North America	100perContinent	1844444	Brazil	South America	Continent Comparison
1781002	Canada	North America	100perContinent	1844422	Brazil	South America	Continent Comparison
1781141	Canada	North America	100perContinent	1847848	Brazil	South America	Continent Comparison
1781252	Canada	North America	100perContinent	1845959	Brazil	South America	Continent Comparison
1781363	Canada	North America	100perContinent	1845545	Brazil	South America	Continent Comparison
1781505	Canada	North America	100perContinent				

Table showing dates of isolation of the serial colony picks

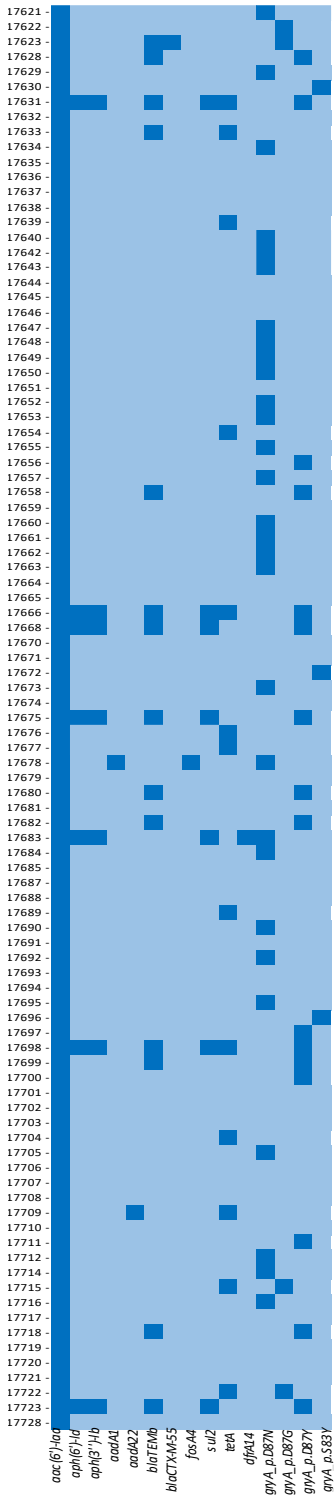
Serial Isolates

PubMLST_ID	Name	Data of isolation
17663	NSW088	25/08/2015
17660	NSW089	25/08/2015
17664	NSW105	24/04/2015
17671	NSW117	27/04/2015
17679	NSW128	09/06/2016
17721	NSW12-075	31/03/2015
17678	NSW139	22/06/2015
17662	NSW092	17/08/2015

Household isolates

PubMLST_ID	Strain ID	Data of isolation
17718	NSW29-087	09/04/2015
17682	NSW177	13/04/2015

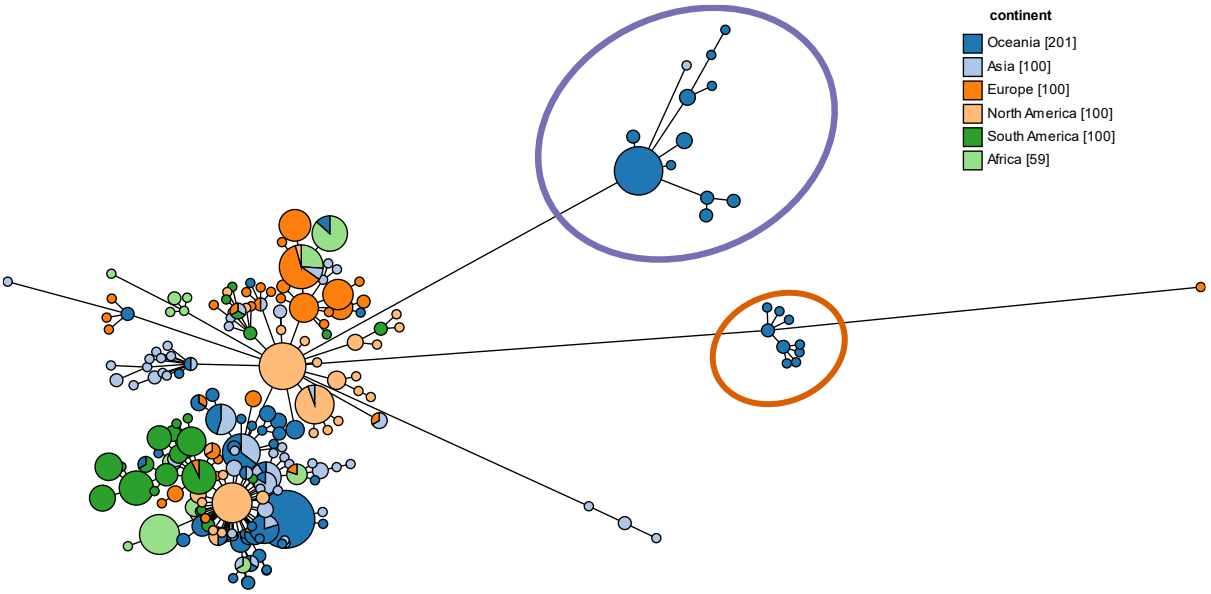
Heatmap of acquired resistance genes and chromosomal point mutation in *gyrA* in the NSW isolates



Acquired resistance genes and chromosomal point mutations within the 95 NSW isolates. Presence of a gene or a point mutation was represented by a dark blue square, while absence was represented by light blue. All isolates had *aac(6')-Iaa*, while some isolates had no further resistance genes or chromosomal point mutations, others had up to 7 resistance genes or chromosomal point mutations.

Minimal spanning tree of the NSW isolates and global representatives

This tree consisted of the same isolates as Figure 3. Oceanian isolates are labelled with dark blue, Asian light blue, European dark orange, North American light orange, South Africa dark green and African light green. Isolates with 20 or fewer allelic differences were collapsed into the same node in order to aid visualisation. Isolate groupings were high congruent with the clades observed in the NJTree of the same isolates (Figure 3). Clade A is highlighted with a purple circle and Clade C with an orange circle, the rest of the isolates belong to Clade B.



Minimal spanning tree of Oceanian isolates and global representatives from Asia (A), Europe (B), North America (C) and South America (D)

The NJTrees were created using cgMLST alleles, all of the trees included the 95 NSW isolates, 191 Queensland isolates and 6 Oceanian isolates. The trees were annotated using country of isolation for all isolates. Isolates with 22 or fewer allelic differences were collapsed into the same node in order to aid visualisation. Clade A is highlighted with a purple circle and Clade C with an orange circle, the rest of the isolates belong to Clade B. The Australian lineage is highlighted with a red circle.

A: Comparison with 200 Asian isolates. This minimal spanning tree is highly congruent with the NJTree of the same isolates (Figure 4a) as Clade B is highly admixed with the exception of the Australian lineage (red circle).

B: Comparison with 200 European isolates. This minimal spanning tree is highly congruent with the NJtree of the same isolates (Figure 4b). Isolates predominantly formed continent specific groupings but admixture was present.

C: Comparison with 200 North American isolates. This minimal spanning tree is highly congruent with the NJtree of the same isolates (Figure 4c). Isolates predominantly formed continent specific groupings, although there were two North American groups (Canada/USA and Mexico/USA) and there was very little admixture.

D: Comparison with 200 South American isolates. This minimal spanning tree is highly congruent with the NJtree of the same isoaltes (Figure 4d). The Clade B Isolates split into clusters with very little admixture, two of which were South American (Chile and Brazil dominiating each) and the Oceanian isolates formed separate distinct clusters.

