



Whole genome SNP analysis of bovine *B. anthracis* strains from Switzerland reflects strict regional separation of Simmental and Swiss Brown breeds in the past



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ABSTRACT

Bacillus anthracis is an evolutionarily young species that presents an extremely low genetic diversity due to its slow mode of propagation, determined by short replication phases and long sporulation periods. In our ongoing efforts to elucidate phylogenetic relationships between European *B. anthracis* isolates, the genomes of five strains from Switzerland belonging to lineages B.Br.CNEVA and A.Br.Aust94 were sequenced. Comparative analysis with additional, available genomes from both lineages, were used to reconstruct the substructure of these populations. Genome-wide single-nucleotide polymorphism analysis revealed two phylogeographical different groups among the Swiss B.Br.CNEVA strains (central and eastern Switzerland), that define the oldest most recent common ancestor of the B.Br.CNEVA lineage currently known. Age-old practices of livestock selection, breeding and preservation of unique traits of local breeds in Alpine valleys have likely favored differentiation of regional *B. anthracis* populations over centuries and the emergence of genetically distinct strains in an otherwise similar environment.

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1. Introduction

Anthrax has a long common history with animals and humans. It has been one of the infectious diseases with major mortality among livestock for several millenium (Turnbull, 2002). During the first part of the 20th century, active control measures and large animal vaccination programs succeeded in reducing the incidence of the disease in Europe. Many European countries are now probably free of anthrax, but the disease persists in regions around the Mediterranean Sea and in Eastern Europe where it almost exclusively affects animals at pasture (Schmid and Kaufmann, 2002; Derzelle and Thierry, 2013). In Switzerland, anthrax was eradicated in cattle in the 1960s by strictly prohibiting the burial of dead animals or slaughtered waste and requiring the burning of the carcasses of animals that died from diseases.

Bacillus anthracis, the etiological agent of anthrax, is a spore-forming bacterium belonging to the *Bacillus cereus* group. The

pathogen spends the majority of its life cycle as a quiescent spore that can persist in soil for decades. All mammals are known to be susceptible to anthrax, but *B. anthracis* primarily affects herbivores, causing acute, often fatal disease in cattle. A tripartite toxin consisting of the edema factor, the lethal factor, and the protective antigen, which serves as adhesive unit for the latter two, is able to cause edema and cell death. Furthermore, the production of a polyglutamic acid capsule allows the organism to escape the immune system and spread in the host organism. Ruminants become infected by ingestion of soil-borne spores while browsing or grazing (Turnbull, 2002; Hugh-Jones and Blackburn, 2009).

As spore-forming bacteria, opportunity for accumulating DNA mutations is limited by the episodic short reproductive cycles interrupted by long dormant phases. *B. anthracis* constitutes therefore a highly monomorphic species with relatively little genetic variation, including single nucleotide polymorphisms (SNPs) (Keim et al., 2009; Pilo and Frey, 2011). With the completion of a growing number of genome sequences, genome-wide comparison of multiple strains has led to major progress in the understanding of the global population structure of the species (Pearson et al., 2004; Van Ert et al., 2007; Simonson et al., 2009). The *B. anthracis* population is composed of three main clades (A, B

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and C), with further subdivisions into 13 lineages and genetic groups (e.g. C.Br.A1055, B.Br.001/002, B.Br.KrugerB, B.Br.CNEVA, A.Br.001/002, A.Br.Ames, A.Br.Australia94, A.Br.003/004, A.Br.Vollum, A.Br.005/006, A.Br.WNA, A.Br.011/009 and A.Br.008/011) (Van Ert et al., 2007). Clade A has known the most dramatic dispersal around the world, with A-lineages recovered from across the five continents. These strains account for the majority (85%) of anthrax cases reported around the world (Keim et al., 2000; Van Ert et al., 2007). Clade B is divided into two genetically distinct branches with geographically limited repartition. Branch B.Br.001/002 (including the derived B.Br.Kruger lineage) is ecologically established in Southern Africa, in particular in the Kruger National Park (South Africa), where it co-exists with strains from clade A, especially of lineage A.Br.Vollum (Smith et al., 2000). The B.Br.CNEVA branch is exclusively found in Europe. Its strains are generally isolated from livestock (Gierczynski et al., 2004; Pilo

et al., 2008; Garofolo et al., 2011; Antwerpen et al., 2012; Steiner et al., 2013; Girault et al., 2014a). The C clade (C.Br.A1055) is an uncommon genetic group of unknown origin. Only four C.Br.A1055 strains are currently known in US collection (Van Ert et al., 2007).

In this study, genome-wide SNP analysis was used to subtype five bovine strains from Switzerland collected in the period 1952–1962. They represent the latest anthrax cases from cattle reported in Switzerland that were preserved. Comparative genomics were conducted using a total of 50 additional strains to get insight into the worldwide phylogenetic placement of the Swiss strains. The trees generated provide new insight on the evolutionary history, local settlement and differentiation of the European-specific B.Br.CNEVA branch and the worldwide A.Br.Aust94 group.

Table 1Whole genome sequences of *B. anthracis* strains used in this study.

Strain	Country	canSNP	year	source	Accession number
Ames Ancestor	USA	A.Br.Ames			NC_007530.2
A0389	Indonesia	A.Br.001/002			NZ_ABLB000000000.1
BA103	Japan	A.Br.001/002		Bovine	DRR000183
08_08_20	France	A.Br.001.002	2008	bovine	NZ_JHCB000000000.2
BA104	Japan	A.Br.Australia94	1982	swine	DRR000184
9080 G	Georgia	A.Br.Australia94	1998	soil	NZ_CM0022398.1
Australia 94	Australia	A.Br.Australia94	1994	bovine	NZ_AAES000000000.1
JF3853	Switzerland	A.Br.Australia94	1952	Bovine	ERR899845
2000031027	USA	A.Br.Australia94	1957	Bos taurus	NZ_JTAR000000000.1
K1285	Namibia	A.Br.Australia94	1996	zebra	NZ_LFYF000000000.1
K1409	Denmark	A.Br.Australia94	1974	cattle	ERR930300
K2883	India	A.Br.Australia94	1997	human	NZ_LFYH000000000.1
K4834	Australia	A.Br.Australia94	1997	bovine	NZ_LFYJ000000000.1
A.Br.003	UK, scotland	A.Br.Australia94		human	NZ_JMPV000000000.1
52 G	Georgia	A.Br.Australia94	2009	bovin	NZ_CM0022395.1
8903 G	Georgia	A.Br.Australia94	1997	soil	NZ_CM0022401.1
A1039	Bolivia	A.Br.003/004	1999	Bos taurus	NZ_LAKZ000000000.1
K8215	Argentina	A.Br.003/004	1996	bovine	NZ_LGIG000000000.1
A1075	Chile	A.Br.003/004		Bos taurus	NZ_LBFE000000000.1
K3	South Africa	A.Br.005/006		human	NZ_CP009331.1
H29	Zambia	A.Br.005/006	2012	human	DRR014739
CZC5	Zambia	A.Br.005/006	2011	hippopotamus	NZ_BAVT000000000.1
PAK-1	Pakistan	A.Br.008/011	1978	sheep	NZ_CP009325.1
Turkey32	Turkey	A.Br.008/011	1991	human	NZ_CP009315.1
Ba4599	UK,Scotland	A.Br.008/011	2009	Human (heroin)	NZ_AGQP000000000.1
99–100	France	A.Br.011/009	1999	bovine	NZ_JHDR000000000.2
Scotland476	UK, Scotland	A.Br.011/009	2006	Animal skin (drum)	SRR2094254
Pollino	Italy	A.Br.011/009	2014	Bos taurus	NZ_CP010813.1
A0193	USA	A.Br.WNA		bovine	NZ_ABFK000000000.1
Canadian_bison	Canada	A.Br.WNA			NZ_CP010322.1
USA6153	USA	A.Br.WNA			NZ_AAER000000000.1
A0488	UK	A.Br.Vollum	1935	cattle	NZ_ABJC000000000.1
Vollum	UK, Scotland	A.Br.Vollum	1963	cow	NZ_CP007666.1
K1129	Pakistan	A.Br.Vollum	1995	Hair goat	NZ_LGIF000000000.1
JF3887	Switzerland	B.Br.CNEVA	1960	Bovine	ERR899847
JF3888	Switzerland	B.Br.CNEVA	1962	Bovine	ERR899848
JF3852	Switzerland	B.Br.CNEVA	1953	Bovine	ERR899844
JF3854	Switzerland	B.Br.CNEVA	1957	Bovine	ERR899846
00–82	France	B.Br.CNEVA	2000	Bovine	NZ_JHDS000000000.2
CNEVA-9066	France	B.Br.CNEVA	1992	Bovine	NZ_AAEN000000000.1
A0465	France	B.Br.CNEVA	1997	bovine	NZ_ABLH000000000.1
BF1	Germany	B.Br.CNEVA	2009	cow	NZ_AMDT000000000.1
RA3	France	B.Br.CNEVA	1998	bovine	NZ_CP009697.1
Kruger B	South Africa	B.Br.Kruger			NZ_AAEQ000000000.1
A0442	South Africa	B.Br.001/002			NZ_ABK000000000.1
SVA 11	Sweden	B.Br.001/002	2011	Cow	NZ_CP006742.1
Zimbabwe89	Zimbabwe	B.Br.001/002			NZ_JMPU000000000.1
HYU01	Korea	B.Br.001/002	2009	soil	NZ_CP008846.1
BA1035	South Africa	B.Br.001/002		human	NZ_CP009700.1
A1055	USA	C.Br.A1055			NZ_AAEO000000000.1
2002013094	USA	C.Br.A1055	1956	soil	NZ_CP009902.1
2000031021	USA	C.Br.A1055		soil	NZ_CP007618.1
2000031052	USA	C.Br.A1055	1956	Bos Taurus	NZ_JSZS000000000.1
AH820	Norway	<i>B. cereus</i>			NC_011773.1

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