

# Plague Denmark Paper

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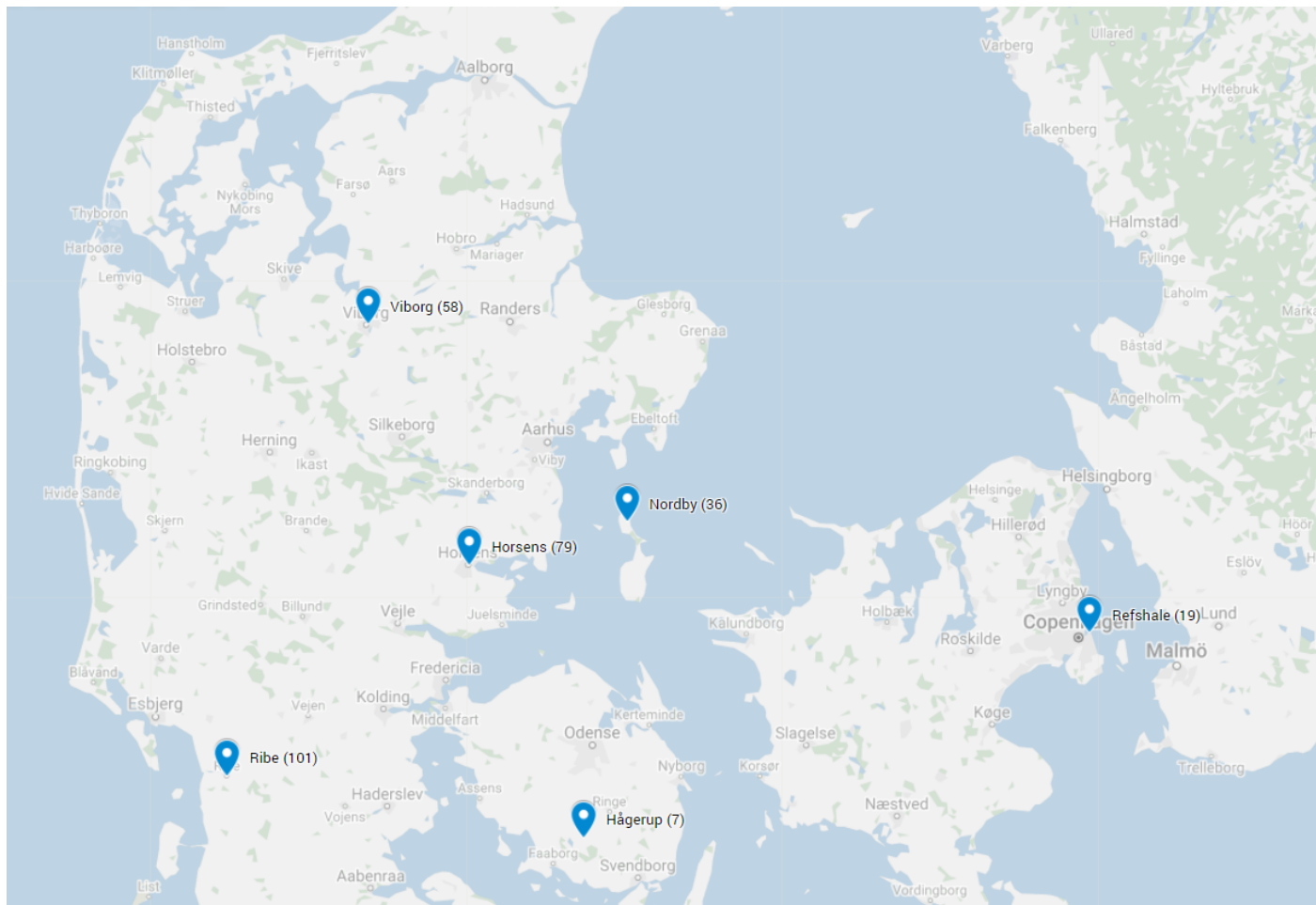
# Data Collection

326 individuals were sampled across 8 municipalities from 14 archaeological sites with occupation dates spanning from 900 to 1600 CE (Table 1). The most heavily represented periods are the Danish early medieval period (1050–1225) and the Danish medieval period (1225–1536) 1.

- Kat's Notes:**
  - Positivity rate (all sites): 4.6% (15/326)
  - Positivity rate (excluding negative sites): 9.4% (15/159)

Table 1: Site summary.

Municipality	Site Name	Site Code	Site Date	Sampled	Plague Positive
Ribe	Ribe Gräbrødre	ASR 1015	1200 : 1560	53	6
	Ribe Lindegården (Vikings)	ASR 13/13II	900 : 1000	15	0
	Ribe Lindegården (City Cemetery)	ASR 13II	1200 : 1560	28	1
	Ribe Lindegården	ASR 2391	900 : 1000	5	0
Nordby	Nordby	FHM 3970	1050 : 1250	36	0
Horsens	Monastery Church	HOM 1272	1600 : 1800	50	0
	Ole Wormsgade	HOM 1649	1100 : 1500	17	2
	Sejet	HOM 1046	1150 : 1574	25	1
	Tirup	VKH 1201	1150 : 1350	12	1
Hågerup	Hågerup	ØHM 1247	1100 : 1555	7	1
Refshale	Refshale	Refshale	1100 : 1350	19	0
Viborg	Sct. Michael	JAH 1-77	1000 : 1529	4	0
	The Catholic Church	VSM 09264	1100 : 1529	6	0
	Sct. Mathias	VSM 855F/906F	1100 : 1529	23	0
	Sct. Drotten	VSM 902F	1100 : 1529	8	0
	Faldborg	VSM 29F	1100 : 1600	17	2
Total				326	15



**Figure 1:** Map Denmark Sites (PLACEHOLDER)

# Plague Detection

13 individuals were identified as plague-positive based on a combination of PCR assays, shotgun sequencing, and targeted enrichment for the *Yersinia pestis* whole genome (Table ?? and ??). 4 individuals had chromosomal coverage insufficient for phylogenetic analysis (<3X mean).

## Kat's Notes:

- Full genomes can only be retrieved from samples with 6/6 positive PCR replicates.
- *Y. pestis* is only detected during the Danish medieval period (1225–1536).
- Are G25A and G25B two individuals from the same grave??

**Table 2:** Plague positive summary.

Arch ID	Project ID	Site Code	PCR	Human (%)	Plague (%)	Chrom	pCD1	pMT1	pPCP1
G16	D71	ASR 1015	6/6	5.95	0.18	22.6	39.4	14.7	4.6
G861 x1035	D75	ASR 1015	6/6	4.42	0.23	17.4	40.2	16.5	3.4
G25B x98	R36	ASR 1015	6/6	8.41	0.25	24.0	51.8	14.9	5.8
G25A	D62	ASR 1015	6/6	1.12	0.10	3.8	10.5	2.5	0.9
G207	D72	ASR 1015	6/6	12.94	0.04	6.0	13.5	5.8	2.2
A19 X21	D24	ØHM 1247	6/6	0.55	0.01	<b>2.6</b>	6.1	1.9	0.7
A146 x3011	P187	HOM 1046	6/6	0.68	0.01	4.9	18.4	6.6	52.2
A1155 x1155	P384	HOM 1649	4/6	0.11	0.01	<b>1.1</b>	4.8	1.4	19.6
A1480 x1480	P387	HOM 1649	6/6	0.04	0.01	6.5	21.7	5.0	75.0
G371	P212	VKH 1201	6/6	0.61	0.04	6.7	26.3	8.5	56.6
Gr GC 15	D51	VSM 29F	6/6	0.67	0.05	9.0	25.4	8.1	2.0
Gr ID 319	R21	VSM 29F	6/6	0.85	0.01	<b>2.6</b>	3.8	2.3	0.4
X1265	P246	ASR 13 II	6/6	0.03	0.01	<b>0.1</b>	0.1	0.1	3.2

**Table 3:** Plague false positive summary.

Arch ID	Project ID	Site Code	PCR	Human (%)	Plague (%)	Chrom	pCD1	pMT1	pPCP1
G70 x212	R44	ASR 1015	3/6	1.48	0.00	0.1	0.1	0.1	0.0
G860	R39	ASR 1015	5/6	0.09	?	?	?	?	?
G364	R43	ASR 1015	4/6	?	?	?	?	?	?
K1167 x1167	P235	ASR 13 II	3/6	?	?	?	?	?	?
A21 x23	D25	ØHM 1247	4/6	0.01	0.00	0.05	0.1	0.0	0.0
G260 K539 x876	R27	VSM 09264	3/6	?	?	?	?	?	?

## Dating

To estimate dates for the plague-positive individuals, a Bayesian Evaluation of Temporal Signal (BETS) was first performed. Briefly, each candidate model was tested using the correct collection dates of all samples and then compared to the same model with all collection dates assumed to be contemporaneous. Bayes factors (BF) were calculated by comparing the marginal likelihoods of each model, as estimated with a generalized stepping stone (GSS) computation across 100 chains each sampled over 1,000,000 generations.

The BETS analysis revealed decisive support for temporal signal (dates vs. no dates) using both the strict clock (SC) and uncorrelated lognormal relaxed clock (UCLN) (Table 4). A comparison of the strict vs. relaxed clocks using collection date produced decisive support for the relaxed clock.

**Table 4:** Bayesian Evaluation of Temporal Signal (BETS) summary.

Model	Abbrev.	Dates	Likelihood	Bayes Factor (Dates)	Bayes Factor (Model)
Strict Clock	SC	Yes	-5948088	749	–
		No	-5948837	–	–
Relaxed Clock	UCLN	Yes	<b>-5947948</b>	715	140
		No	-5948663	–	–

A time-scaled phylogeny with tip-dating was estimated using a relaxed clock and diffuse normal priors centered around the mean collection date. The tip dates from the 9 high coverage *Y. pestis* genomes are presented in Table 5 as the 95% highest posterior density (HPD) intervals.

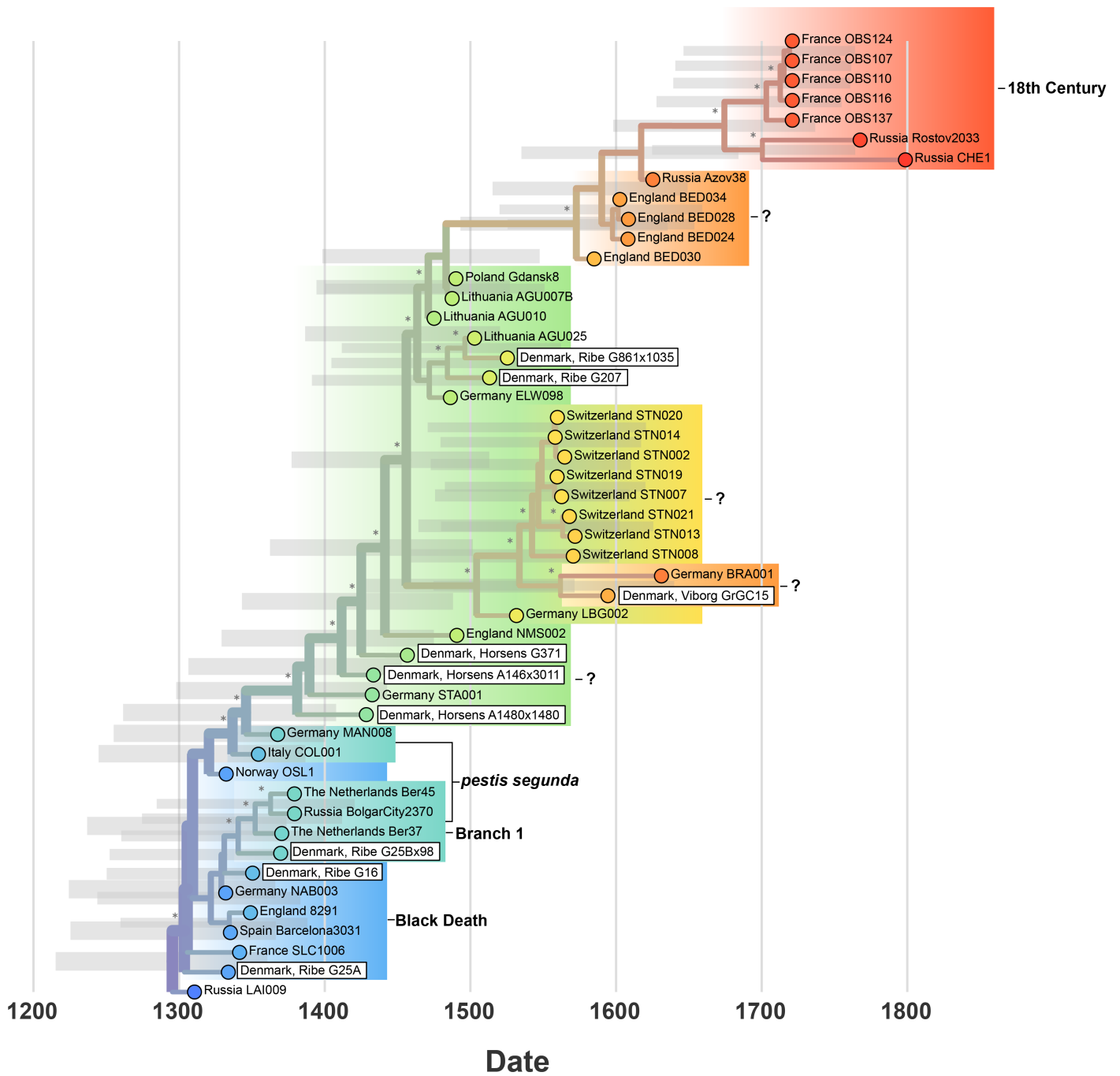
All estimated tip dates had overlap with the expected range of site occupation dates, with the exception of G371 (P212) from the site of Tirup (VKH 1201).

**Table 5:** Tip-dating summary.

ID	Site Code	Site Occupation	Arm Position Date	Tip Date	Haplotype
G16	ASR 1015	1200 : 1560	1250 : 1450	1310 : 1388	U2e2a1a
G861 x1035	ASR 1015	1200 : 1560	1350 : 1450	1489 : 1567	I1f
G25B x98	ASR 1015	1200 : 1560	1350 : 1450	1327 : 1414	–
G25A	ASR 1015	1200 : 1560	1350 : 1450	1295 : 1375	H7b2
G207	ASR 1015	1200 : 1560	1350 : 1450	1477 : 1551	H1a3c1
A146 x3011	HOM 1046	1150 : 1574	1250 : 1350	1397 : 1470	–
A1480 x1480	HOM 1649	1100 : 1500	?	1384 : 1473	–
G371	VKH 1201	1150 : 1350	1250 : 1350	1419 : 1490	–
Gr GC 15	VSM 29F	1100 : 1600	1350 : 1450	1539 : 1655	V12

# Phylogeny

The time-scaled phylogeny reveals geographic and temporal structure during the Second Pandemic (Figure 2).



**Figure 2:** Bayesian time-scaled phylogeny.

### Phase 1: 1300-1450

- All *Y. pestis* genomes from the 14th century cluster together.
- Samples from the early-mid 1300s are widely dispersed across Europe (Figure 3), and have highly similar genetic content resulting poorly resolved branching order. This suggests rapid, epidemic spread, thought to be associated with the Black Death.
- Samples from the late 1300s also cluster together, and are linked to the *pestis segunda* series of epidemics in Europe.
- The only Danish samples in Phase I are from Ribe, and fall within both the Black Death and *pestis segunda* groups. - These are primarily coastal sites, Germany and Russia as the exception.

### Phase 2: 1450-1600

- A very curious branching pattern, lots of 'independent' emergences rather than monophyletic clades.
- All Danish samples from the Horsens region fall here, and although they have temporal overlap with each other, the lineages of plague are distinct.
- ...

### Phase 3: 1600-1800

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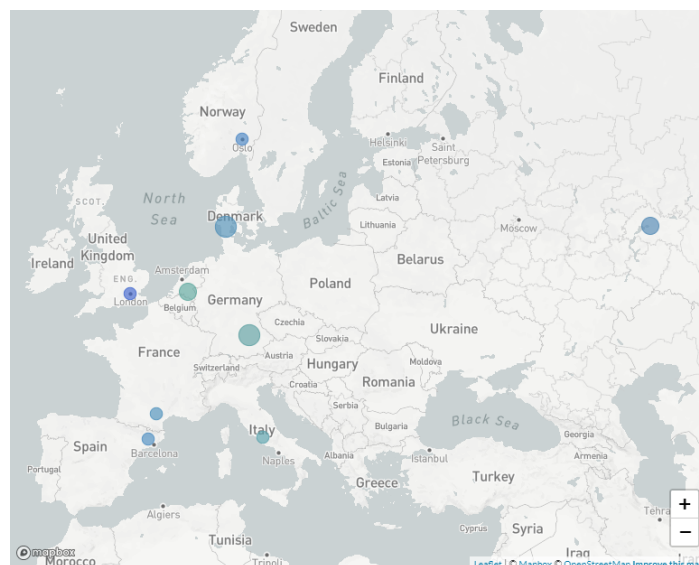
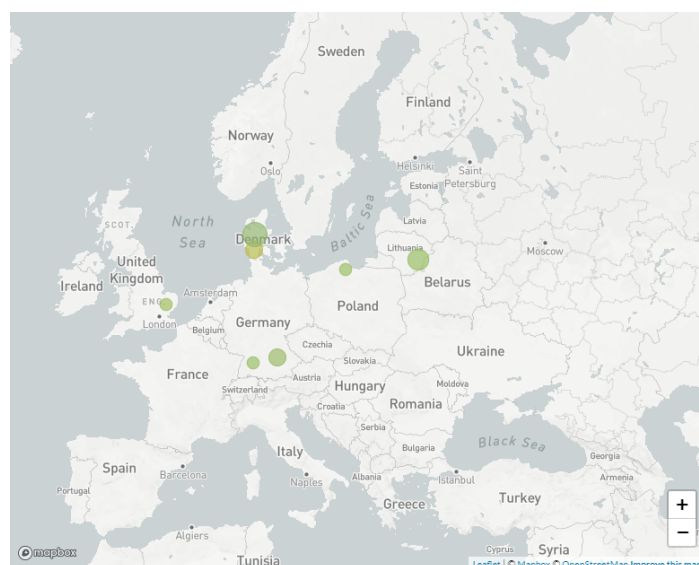
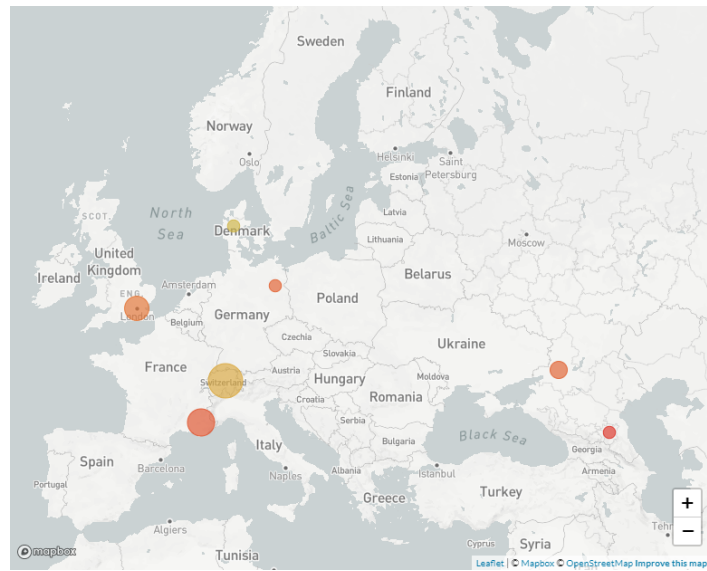


Figure 3: Phase 1: 1300 - 1450



**Figure 4:** Phase 2: 1450 - 1600



**Figure 5:** Phase 3: 1600 - 1800



## References

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