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 900-1600 CE (Table [1](#)). The most heavily represented periods are the Danish early medieval period (1050–1225) and the Danish medieval period (1225–1536) [1].

Table 1: Site summary.

Municipality	Site Name	Site Code	Site Date	Excavated	Sampled	Plague Positive
Ribe	Ribe Gräbrødre	ASR 1015	1200:1560	915	53	6
	Ribe Lindegården (Vikings)	ASR 13 II	900:1000	10	?	0
	Ribe Lindegården (City Cemetery)	ASR 13 II	1200:1560	113	?	1
	Ribe Lindegärden	ASR 2391	1200:1560	183	6	0
Nordby	Nordby	FHM 3970	1050:1250	126	36	0
Sejet	Sejet	HOM 1046	1150:1574	435	25	1
Horsens	Monastery Church	HOM 1272	1600:1800	221	50	0
	Ole Wormsgade	HOM 1649	1100:1500	578	17	2
	Tirup	VKH 1201	1150:1350	574	12	1
Hågerup	Hågerup	ØHM 1247	1100:1555	?	7	1
Refshale	Refshale	Refshale	1100:1350	303	19	0
Viborg	Sct. Michael	JAH 1-77	1000:1529	285	4	0
	The Catholic Church	VSM 09264	1100:1529	95	6	0
	Sct. Mathias	VSM 855F/ 906F	1100:1529	280	23	0
	Sct. Drotten	VSM 902F	1100:1529	84	8	0
	Faldborg	VSM 29F	1100:1600	80	17	2
Total			900:1600		326	15

Plague Detection

15 individuals were identified as plague-positive based on a combination of PCR assays, shotgun sequencing, and targeted enrichment for the *Yersinia pestis* whole genome {#tbl:plague_positive_summary}. 9 individuals had coverage levels sufficient for phylogenetic analysis as determined by having 50% of the chromosome covered by at least 3X (Table ??).

Table 2: Plague positive summary. Replicon statistics represent the mean fold coverage.

Arch ID	Project ID	Site Code	PCR Replicates	Human (%)	Plague (%)	Chromosome	pCD1	pMT1	pPCP1
GrGC15	D51	VSM 29F	6/6	0.67	0.05	9.04	25.4	8.12	1.97
GrID319	R21	VSM 29F	6/6	0.85	0.01	2.60	4.75	2.28	0.43
A146x3011	P187	HOM 1046	6/6	0.68	0.01	4.91	18.4	6.63	52.19
G371	P212	VKH 1201	6/6	0.61	0.04	6.71	26.25	8.50	56.64
A1155x1155	P384	HOM 1649	4/6	0.11	0.01	1.10	4.83	1.41	19.55
A1480x1480	P387	HOM 1649	6/6	0.04	0.01	6.55	21.67	4.99	75.00
A21x23	D25	ØHM 1247	4/6	0.01	0.00	0.04	0.11	0.02	0
G25A	D62	ASR 1015	6/6	1.12	0.10	3.83	10.48	2.48	0.86
G16	D71	ASR 1015	6/6	5.95	0.18	22.95	39.38	14.69	4.56
G207	D72	ASR 1015	6/6	12.94	0.04	5.95	13.53	5.82	2.18
G861x1035	D75	ASR 1015	6/6	4.42	0.23	17.42	40.23	16.48	3.40
G25Bx98	R36	ASR 1015	6/6	8.41	0.25	24.01	51.80	14.93	5.75
G70x212	R44	ASR 1015	3/6	1.48	0.00	0.06	0.11	0.05	0.01
X1265	P246	ASR 13 II	6/6	0.03	0.01	0.12	0.47	0.10	3.2

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 3). A comparison of the strict vs. relaxed clocks using collection date produced decisive support for the relaxed clock.

Table 3: 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	**-5947948**	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 fro the 9 high coverage *Y. pestis* genomes are presented in Table 4 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 4: Tip-dating summary.

Project ID	Site Code	Site Occupation	Tip Date	Overlap
D51	VSM 29F	1100 : 1600	1539 : 1655	Yes
P187	HOM 1046	1150 : 1574	1397 : 1470	Yes
P212	VKH 1201	1150 : 1350	1419 : 1490	No
P387	HOM 1649	1100 : 1500	1384 : 1473	Yes
D62	ASR 1015	1200 : 1560	1295 : 1375	Yes
D71	ASR 1015	1200 : 1560	1310 : 1388	Yes
D72	ASR 1015	1200 : 1560	1477 : 1551	Yes
D75	ASR 1015	1200 : 1560	1489 : 1567	Yes
R36	ASR 1015	1200 : 1560	1327 : 1414	Yes

Phylogeny

The time-scaled phylogeny reveals geographic and temporal structure during the Second Pandemic (Figure 1). This study recapitulates the finding that *Y. pestis* genomes sampled from the 14th century all cluster together. The branching pattern of samples dating to the first half of the 14th century are poorly resolved, due to extremely similar genetic content. However, this - Large geographic spread, Italy -> Norway, Spain -> Eastern Russia.
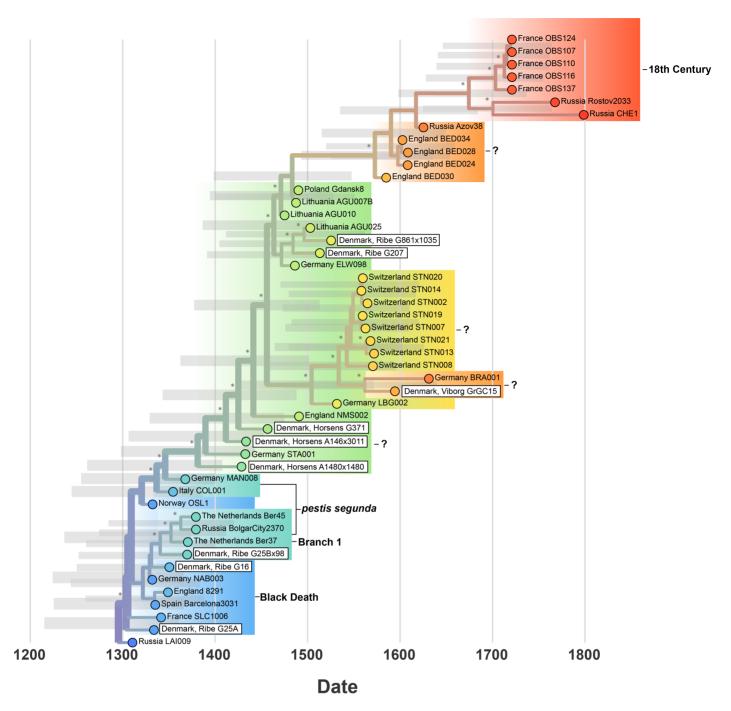
Figure 1: Bayesian time-scaled phylogeny.

1300-1450	1450-1600	1600-1800
!Map Black Death and pestis segunda.png	!Map Phase 2.png	!Map Phase 3.png

1. **A millennium of population change in pre-modern Danish Ribe**
   Dorthe Dangvard Pedersen, Peter Tarp, Morten Søvsø, Hans Christian Petersen, George Robert Milner, Jesper Lier Boldsen
   Anthropologischer Anzeiger (2020-02-13) http://www.schweizerbart.de/papers/anthranz/detail/77/91627/A_millennium_of_population_change_in_pre_modern_Da?af=crossref
   DOI: 10.1127/anthranz/2019/0952