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CHALLENGES OF ANCIENT DNA PRESERVATION IN FINLAND: A REPORT ON UNSUCCESSFUL SAMPLES

Abstract

Ancient DNA (aDNA) research has rapidly expanded our understanding of past populations, yet its success remains highly dependent on biomolecular preservation. This article presents negative sampling outcomes from 85 individuals in Finland, sampled between 2017 and 2022. These individuals represent sampling efforts that failed to yield data for human population genetic analyses, corresponding to a success rate of approximately 44%. The failed dataset includes samples from a wide temporal and geographical range, from Bronze Age contexts to post-medieval burials, and notably, some of Finland's most iconic archaeological individuals. Our findings align with previous studies and show that the petrous part of the temporal bone and teeth consistently outperform other skeletal elements in human DNA preservation. Preservation also varied by region, and possibly also by burial environment and post-excavation storage history.

Keywords: aDNA, sampling strategies, DNA preservation, DNA degradation

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INTRODUCTION

Ancient DNA (aDNA) research has increased our understanding of past populations and individuals, but its success depends on DNA preservation. In response to both the promise and the limitations of this field, several initiatives have been launched to explore genetic histories across different regions. One such effort is the Sugrige project, an interdisciplinary research initiative launched in 2016 with the aim of collecting aDNA samples from North-western Eurasia to study the genetic history of Uralic-speaking populations. The work started in the Sugrige project is continued in the Sumragen project that focuses on Iron Age individuals in Finland, as well as in Human Diversity, an interdisciplinary University of Turku Profilation Profi7 project (https://sites.utu.fi/humandiversity/).

The research outputs of Sugrige/Sumragen have addressed several areas of aDNA research. These include reconstructions of population movements and interactions over time (Lamnidis et al. 2018; Översti et al. 2019; Peltola et al. 2023; Nordfors et al. 2025a), the study of individual life histories by combining archaeological, genetic, and historical evidence (Moilanen et al. 2022b; Rohrlach et al. 2024; Nordfors et al. 2025b; Peltola et al. in prep.), and contributions to the study of ancient pathogens (Majander et al. 2020; Kocher et al. 2021; Michel et al. 2024).

Many of the project's samples have provided valuable genetic data from ancient humans, including pathogen DNA, that contribute to ongoing and future studies. However, several samples have not yielded usable genetic data. Between October 2017 and August 2022, a total of 193 individuals were sampled – some from different skeletal elements – at the Max Planck Institute for the Science of Human History (now Max Planck Institute for Geoanthropology) in Jena, Germany. Of these individuals, 85 yielded DNA data suitable for human population genetic analyses, resulting in a success rate of approximately 44%.

In this paper, we report the previously unpublished set of samples that failed to yield sufficient genetic data (Table 1, SI, Fig. 1). These negative results provide valuable information for future sampling, as they clarify whether particular individuals or skeletal elements have already been sampled, how, when, and where the DNA analysis was done and what methods were used in the laboratory. This information helps other researchers decide whether these individuals or skeletal elements should be re-analysed in the future using improved techniques. The reporting also responds to the public interest in aDNA research, such as frequent inquiries about specific sampled individuals and sites. Additionally, we use the dataset at hand to explore potential factors that may play a role in favourable DNA preservation in Finland, which helps researchers to make better-informed decisions for sampling new sites and individuals in the future.

While the general principles of aDNA preservation are quite well established, systematic data on retrieval success from Finnish archaeological contexts remain unpublished. The environmental and cultural conditions in Finland (acidic soils and a long tradition of cremation) pose challenges distinct from many other European regions. By presenting a comprehensive dataset of unsuccessful samples alongside the successful ones, our study provides quantitative success rates, site-level comparisons, and skeletal element-specific outcomes that are essential for refining sampling strategies in low-preservation environments.

MATERIALS AND METHODS

Sampling was conducted at the aDNA facility at the Max Planck Institute of Geoanthropology (formerly the MPI for the Science of Human History) between October 2017 and August 2022). Skeletal elements selected for sampling were briefly exposed to UV light to reduce surface contamination, and bone powder was drilled from the samples for DNA extraction (Neumann et al. 2020; Orfanou et al. 2020).

DNA was extracted from the bone powder following a manual protocol (Dabney et al. 2013; Velsko et al. 2020). In brief, c. 50 mg of bone powder was combined with an extraction buffer containing 0.45 M EDTA and 0.25 mg/ml proteinase K, and the reactions were incubated at 37 °C on rotation overnight, after which DNA was purified in silica columns. Since 2020, an automated protocol has been used (Rohland et al. 2018), with purification from 150 ml of lysate using silica-coated magnetic beads and binding buffer D.

DNA extracts were converted into Illumina sequencing libraries. Before autumn 2020, the manual double-stranded protocol described in Meyer and Kircher (2010) and Aron et al. (2020) was used. DNA was treated with uracil-DNA-glycosylase to partially remove post-mortem DNA damage (UDG-half). Libraries were tagged with sample-specific indices to allow for parallel sequencing (Kircher et al. 2012). In autumn 2020, extraction and library preparation protocols were updated to automated protocols, and the standard library build was changed from double-stranded UDG-half to a single-stranded protocol without UDG treatment, described in Gansauge et al. (2017; 2020).

Libraries were sequenced on Illumina HiSeq 4000 or HiSeq 2500 to ~5 million reads, with paired-end or single-end setups, to assess DNA preservation. In the bioinformatic processing, adapter sequences were removed with leeHom (Renaud et al. 2014), and the sequencing reads were mapped to the human reference genome hs37d5 using bwa aln (Li & Durbin 2010), with parameters adjusted for aDNA (-n 0.01 -o 2 -l 16500). The fraction of C-to-T transitions in the terminal positions of the fragments was calculated to allow for qualitative estimation of DNA authenticity.

For most of the project, the cut-off for sufficient DNA preservation was 0.1 % of endogenous DNA, i.e. reads mapping to the human genome, which nearly all of the samples presented here failed to reach. In three cases, non-UDG libraries passed the endogenous DNA threshold but were excluded due to a lack of deamination, which we expected to be ≥5% in non-UDG libraries. In a handful of cases, samples with lower endogenous DNA% (0.05-0.1%) were passed on to human DNA capture (Fu et al. 2015; Mathieson et al. 2015) if the sample was of special interest. This was the case for 16 samples; only three produced usable data (≥20,000 genome-wide markers out of the 1,24M markers covered by the capture panel). Moreover, at least one of the three showed signs of contamination. We also report five samples that exceeded the cutoff for endogenous DNA% yet failed to yield usable data after capture.

To assess the effects of a combination of factors that may contribute to human DNA preservation in Finland, we used a generalised linear mixed model. We included skeletal element, sample age, and library build as explanatory variables with fixed effects on successful human DNA recovery, and archaeological site as a random effect. For simplicity, we modelled DNA recovery as a binary outcome (success/failure), so the results reflect the likelihood of obtaining any amount of analysable human DNA and do not take into account variation in data quality among successful samples.

FAMOUS FINDS

The samples that did not have sufficient human DNA preservation for genetic analyses include some of Finland’s most iconic archaeological finds, such as the Viking Age (c. 800–1050 CE) grave 56 from Eura Luistari, known as the burial of the "Eura matron" (sample IDs LUI002 and LUI027), and an Early Medieval (c. 1050–1250 CE) grave 1/1893 at Perniö Yliskylä (now part of the Salo municipality) (sample PYL005). Both graves have been used as the basis for reconstructions of Iron Age Finnish dress – the Eura and Perniö costumes, which play an important role in public representations of the country's Late Iron Age (Mäkelä & Kunnas 2025). A later costume reconstruction, the so-called Masku costume, is based on grave 32/1925 at Masku Humikkala (Tomanterä 1984). The sample (MAH010.A) from this grave has also failed to yield DNA.

Another famous example is grave 30/1955 at the Medieval cemetery of Mikkeli Visulahti. It is an undated cattle grave known in literature as the "sacrificial ox of Mikkeli" (Fig. 2) (Leppäaho 1957: 16 - 17; Kivikoski 1961: 271; Taavitsainen 1990). While Taavitsainen (1990) has interpreted the find as possibly post-medieval and unrelated to the cemetery, Kivikero (2011: 16) has argued that the preservation of the animal does not differ from the site's Iron Age remains. A human mandible with teeth – possibly from a disturbed burial – was found directly beneath the ox skull during excavation. However, no usable DNA

Table 1. List of archaeological human bone samples from Finland that have failed to yield usable aDNA. The table does not include repeat extraction attempts from the same sample. These, along with additional contextual and technical details, are provided in the Supplementary Table. Chronological abbreviations used: BA - Bronze Age (c. 1500 - 500 BCE), RP = Roman Period (c. 1–400 CE), MiP = Migration Period (c. 400–600 CE), EIA = Early Iron Age (c. 500 BCE–700 CE) MeP = Merovingian Period (c. 600–800 CE), VA = Viking Age (c. 800–1050 CE), LIA - Late Iron Age (c. 700–1100 CE) EM = Early Medieval (c. 1100–1250 CE), M = Medieval (c. 1250–1550 CE), PM = Post-Medieval (1550–).

Municipality	Site	Context	Dating	Museum ID	Sample ID	Sampled Bone
Åland, Eckerö Storby	Ec 6.32	Cairn	EIA	ÅM 235:1	MEL001	Two hand phalanges
Åland, Eckerö Storby	Ec 6.32	Cairn	EIA	ÅM 235:5	MEL003.A	Permanent molar
Åland, Eckerö Storby	Ec 6.32	Cairn	EIA	ÅM 235:5	MEL003.B	Permanent incisor
Åland, Eckerö Storby	Norra gravfältet i Västra Nabbergen, E 6.6	Cairn	EIA	ÅM 176:12a	MEL004.A	Femur
Åland, Eckerö Storby	Norra gravfältet i Västra Nabbergen, E 6.6	Cairn	EIA	ÅM 176:12b	MEL005.A	Femur
Åland, Eckerö Storby	Norra gravfältet i Västra Nabbergen, E 6.6	Cairn	EIA	ÅM 176:13	MEL006.A	Talus
Åland, Finström Godby	Fi 8.11	Mound cemetery	LIA	ÅM 525:118	GBV002.A	Femur
Åland, Saltvik Långbergsöda	Glamilders, Sa 20.8	Stone Age settlement site	3300– 2300 BCE	KM 4784:524	GLA001.A	Phalanx hand
Åland, Saltvik Långbergsöda	Glamilders,Sa 20.8	Stone Age settlement site	3300– 2300 BCE	KM 8679:229	LAB001.A	Femur
Eura	Eläinlääkärin tontti 50010026	Inhumation	MeP	KM 9411:5	EUR001.A	FDI 17
Eura	Vanha kansakoulu (Kaunismäki) 50010016	Grave 17/1987	LIA	KM 24007:123	EU1003.A	Cranium
Eura	Vanha kansakoulu (Kaunismäki) 50010016	Grave 7/1987	LIA	KM 24007:112	EU1004.A	Pars petrosa
Eura	Käräjämäki-Osmanmäki 50010027	Inhumation	LIA	KM 2700:37	KR1001.A	Phalanx foot
Eura	Käräjämäki-Osmanmäki 50010027	Inhumation	LIA	KM 4633:156	KR2002.A	Phalanx hand
Eura	Käräjämäki-Osmanmäki 50010027	Inhumation	LIA	KM 4633:101	KR2002.A	Ulna
Eura	Käräjämäki-Osmanmäki 50010027	Grave 6/1912 (Double burial)	LIA	KM 6127:30	KR3001.A	Cranium

Municipality	Site	Context	Dating	Museum ID	Sample ID	Sampled Bone
Eura	Käräjämäki-Osmanmäki 50010027	Grave 2/1912	LIA	KM 6127:55	KR3002.A	Fibula
Eura	Käräjämäki-Osmanmäki 50010027	Grave 5/1966	MeP	KM 17250:345	KR4001	Two hand phalanges
Eura	Luistari 50400001	Grave 335 (Possibly a triple burial)	MeP	KM 18000:3777	LUI001.A	Pars petrosa
Eura	Luistari 50400001	Grave 56 (Eura matron)	VA	KM 18000:1776	LUI002.A	Pars petrosa
Eura	Luistari 50400001	Grave 56 (Eura matron)	VA	KM 18000:1776:1	LUI027.A	Premolar
Eura	Luistari 50400001	Grave 295 (possibly a multiple burial)	VA	KM 18000:3450	LUI028.A	FDI 37
Eura	Luistari 50400001	Grave 20	MeP	KM 18000:1231	LUI029.A	Humerus
Eura	Luistari 50400001	Grave 285	VA	KM 18000:3269	LUI030.A	FDI 37
Eura	Luistari 50400001	Grave 30	MeP	KM 18000:1394	LUI031.A	Femur
Eura	Luistari 50400001	Grave 95	VA	KM 18000:2095	LUI032.A	Mandible
Eura	Luistari 50400001	Grave 435	MeP/LIA	KM 22346:41	LUI033	Pars petrosa
Eura	Luistari 50400001	Grave 998	MeP	KM 25480:624	LUI034	Pars petrosa
Eura	Luistari 50400001	Grave 331	MeP	KM 18000:3748	LUI037	Phalanx hand
Eura	Luistari 50400001	Grave 1062	MeP	KM 26695:25	LUI038	Phalanx hand
Eura	Pappilanmäki	Grave 20/1939	LIA	KM 11063:764 or 762	EUP001.A	Radius
Eura	Pappilanmäki	Grave 4/1939	LIA	KM 11063:300	EUP002.A	Ulna
Eura	Pappilanmäki	Grave 9/1939	LIA	KM 11063:569	EUP003.A	Phalanx hand
Eura	Yli-Nuoranne	Grave 2/1965	LIA	KM 16950:72	YLI001	Tibia
Eura	Yli-Nuoranne	Grave 3/1965	LIA	KM 16950:134	YLI002	Phalanx hand
Hattula	Myllymäki	Possibly an Iron Age settlement	LIA	KM 19704:1021	MYL002.A	Permanent molar
Hattula	Ruskeenkärki 82010021	Cairn	VA	KM 13777:6	RSK003.A	Pars petrosa
Hattula	Ruskeenkärki 82010021	Cairn	VA	KM 13777:6	RSK003.B	Long bone
Hämeenlinna	Eerola 2 855010004	Cairn	-	KM 22185:1	HME001.A	Cranium
Helsinki	Senaatintori	Grave 238	PM	NA	HKI006.A	FDI 47

Municipality	Site	Context	Dating	Museum ID	Sample ID	Sampled Bone
Ii	Illinsaari Suutarinniemi 1000019094	Grave 2/2013	EM	KM 39519:227/231	ILS003.A	Humerus
Ii	Illinsaari Suutarinniemi 1000019094	Grave 14/2014	EM	KM 40370:137	ILS004	Two permanent molars
Ii	Illinsaari Suutarinniemi 1000019094	Grave 12/2014	EM	KM 40370:135	ILS005.A	Pars petrosa
Isokyrö	Niemenmaanmä-ki 152010008	Cairn	MiP	KM 10851:8	NMM001.A	FDI 32
Joensuu	Kousanniemi Ol-lukkala 45010005	Stray find	PM	KM 28707:6	OLL001.A	Radius
Joroinen	Kalmasaari 1000015010	Burial island	PM	KM 20578:1	JOR001.A	FDI 47
Kaarina	Ristimäki I-II 853010004	Inhumation	LIA	KM 14349:50	RIT001.A	Cranium
Kemiönsaari	Jordbro 40010015	Cairn	BA?	KM 2503A:22	DRF001.A	FDI 27
Kokemäki	Leikkimäki (Äimälä) 271010038	Inhumation or unsuccessful cremation	LIA	KM 2294:30	KLM001	Femur
Kokemäki	Perävainionmäki 271010015	Cairn 1	LIA?	SatM 17824:57	KOI002.A	FDI 47
Kuopio	Kuusikkolahden-niemi 297010010	Cairn	BA	KuM 6154:21:6	KUO001	Phalanx hand
Masku	Humikkala 481010002	Grave 31/1925	EM	KM 8656:31:1a	MAH001.A	Cranium
Masku	Humikkala 481010002	Grave 21/1925	EM	KM 8656:6	MAH002.A	FDI 45
Masku	Humikkala 481010002	Grave 41/1925	EM	KM 8656:5	MAH003.A	FDI 17
Masku	Humikkala 481010002	Grave 44/1925	EM	KM 8656:16	MAH004.A	Tibia
Masku	Humikkala 481010002	Grave 22/1925	EM	KM 8656:1	MAH005.A	Cranium
Masku	Humikkala 481010002	Grave 16/1925	EM	KM 8656:11	MAH006.A	Tarsal bone
Masku	Humikkala 481010002	Grave 9/1925	EM	KM 8656:18	MAH009.A	Femur
Masku	Humikkala 481010002	Grave 32/1925	EM	KM 8656:2	MAH010.A	Cranium
Masku	Humikkala 481010002	Grave 46/1925	EM	KM 8656:1	MAH012.A	FDI 36
Masku	Humikkala 481010002	Grave 35/1925	EM	KM 8656:2	MAH013.A	Pars petrosa
Masku	Humikkala 481010002	Grave 30/1925	EM	KM 8656:15	MAH014.A	Tibia

Municipality	Site	Context	Dating	Museum ID	Sample ID	Sampled Bone
Masku	Humikkala 481010002	Grave 1/1966	EM	KM 16575:32	MAH015.A	Cranium
Mikkeli	Visulahti kalmisto 491010003	Grave 3/1954	EM	KM 13441:43	MK1001	Long bone
Mikkeli	Visulahti kalmisto 491010003	Grave 4/1955	EM	KM 13769:1	MK2002	FDI 48
Mikkeli	Visulahti kalmisto 491010003	Grave 30/1955	EM	KM 13769:182	MK2007	FDI 15
Mikkeli	Visulahti kalmisto 491010003	Grave 29/1955	EM	KM 13769:176	MK2008	Ulna
Nakkila	Penttala 531010020	Inhumation	RP	KM 5851:68	NAP001.A01	Pars petrosa
Nakkila	Penttala 531010020	Inhumation	RP	KM 5851:127	NAP002.A	FDI 48
Nakkila	Penttala 531010020	Inhumation	RP	KM 5577:32	NAP003.A	FDI 18
Nokia	Hakamäki 536010021	Grave 1/1922	EM	KM 8037:4	PRK002	Cranium
Närpiö	Edsbacken 545010013	Cairn, Grave 10	RP, Mip	KM 10888:25	NED001.A	FDI 16
Pori	Leppänen 609010011	Cairn	RP	SatM 17319:7b	POI1001.A	Femur
Pori	Leppänen 609010011	Cairn	RP	SatM 17319:16	PO1002.A	Femur
Pori	Leppänen 609010011	Cairn	RP	SatM 17319:37	PO2001.A	Tibia
Porvoo	Pikku Linnamäki 612010025	Grave 5/1967	RP	KM 17446:4	PPL001	Ulna
Porvoo	Pikku Linnamäki 612010025	Grave 4 or 5	RP	KM 17145:13c	PPL002	Ulna
Pälkäne	Kokkostenkärki 635010024	Cairn	-	KM 9120:12	PKK001.A	Femur
Pälkäne	Kokkostenkärki 635010024	Cairn	-	KM 9221:55	PKK002.A	Cranium
Raasepori	Kroggårdsmal-men 220010058	Tarand grave 4/1937	RP	KM 10612:28	RAS001.A	FDI 18
Raasepori	Kroggårdsmal-men 220010058	Tarand grave 1/1932	RP	KM 9536:3	RAS002.A	Radius
Raisio	Kansakoulunmäki 680010001	Grave 12/1959	EM	KM 14676:271	RK2001.A	Femur
Raisio	Kansakoulunmäki 680010001	Grave 7/1959	EM	KM 14676:241	RK2005.A	FDI 16
Raisio	Kansakoulunmäki 680010001	Grave 23/1960	EM	KM 15357:31	RK3001.A	Femur
Raisio	Kansakoulunmäki 680010001	Grave 21/1960	EM	KM 15357:27	RK3002.A	Pars petrosa
Raisio	Kansakoulunmäki 680010001	Grave 24/1960	EM	KM 15357:44	RK3003.A	FDI 45

Municipality	Site	Context	Dating	Museum ID	Sample ID	Sampled Bone
Raisio	Kansakoulunmäki 680010001	Grave 24/1960	EM	KM 15357:51	RK3004.A	Femur
Raisio	Tuomala 680010008	Inhumation	LIA	KM 19000:8776	RAI001.A	Pars petrosa
Salo (Perniö)	Yliskylän hautausmaa 586010010	Grave 5/1893	EM	KM 2912:87	PYL001	Ulna
Salo (Perniö)	Yliskylän hautausmaa 586010010	Grave 1/1893	EM	KM 2912:48	PYL005	Tarsal bone
Salo (Perniö)	Yliskylän hautausmaa 586010010	Grave 6/1893	EM	KM 2912:92	PYL007	Vertebra
Salo (Perniö)	Yliskylän hautausmaa 586010010	Grave 7/1893	EM	KM 2912:107	PYL008	Tibia
Salo (Halikko)	Rikalanmäki 73010022	Grave F/1950	EM	KM 12690:160	SIK002	FDI 46
Salo (Halikko)	Rikalanmäki 73010022	Grave E/1950	EM	KM 12690:126	SIK003	Scapula
Salo (Halikko)	Rikalanmäki 73010022	Grave V/1950	EM	KM 12690:345	SIK004	Femur
Salo (Halikko)	Rikalanmäki 73010022	Grave Ö/1950	EM	KM 12690:430	SIK005	Radius
Salo (Halikko)	Rikalanmäki 73010022	Grave 2/1953	EM	KM 13298:26	SIK006	Femur
Salo (Halikko)	Rikalanmäki 73010022	Grave 7/1953	EM	KM 13298:145	SIK007	Tibia
Sauvo	Korvala 738010025	Grave 2/1996	RP	KM 29710:20	SAU001.A	Radius
Sauvo	Korvala 738010025	Grave 1/1996	RP	KM 29710:4	SAU002.A	Radius
Turku	Virusmäki 853010014	Inhumation	LIA-EM	KM 6659:73	TUV001.A	Femur
Uusikaarlepyy	Helgobacken	Cairn	BA?	KM 9952	HGB001.A	Tooth unspecified
Valkeakoski	Kiiliä 908010002	Grave 2/1935	LIA-EM	KM 10201:9	VAK001	Mandible
Valkeakoski	Kiiliä 908010002	Grave 1/1913	LIA-EM	KM 6370:206	VAK003	Pars petrosa
Valkeakoski	Muuntajanmäki 908010029	Grave 1/1990	LIA-EM	KM 26079:329	VLM001	Tooth unspecified
Vöyri	Sandbacka-Låg-peld 944010029	Cairn	RP-MiP	KM 7589:10	VLN005.A	Humerus
Ceded Karelia, Sakkola	Lapinlahti, Naskalinmäki	Inhumation	EM-M	KM 7291:31	SA1001.A	Cranium
Russian Karelia, Vitele	Pirdoila	Grave 4/1943	EM-M	KM 11367:57	VIT001.A	Ulna
Russian Karelia, Vitele	Pirdoila	Grave 1/1943	EM-M	KM 11367:18	VIT002.A	Metatarsus

was recovered from the sample (MK2007) taken from one of these human teeth.

We have also sampled individuals from the Late Iron Age (c. 700–1100 CE) multiple burials at Eura Luistari, which Lehtosalo-Hilander (2000: 156) has linked to a possible epidemic. However, no usable DNA - human or pathogen - was recovered from these remains. If pathogen DNA were preserved, Lehtosalo-Hilander's hypothesis could be explored more thoroughly (c.f. Margaryan et al. 2018; Spyrou et al. 2019).

Inhumation burials dating to the Roman Period (c. 1–400 CE) have been of particular importance in the history of Finnish archaeology. In the early 20th century, they were seen as a key to understanding the origins of the Finnish population. The burials were interpreted as evidence of the "first Finns" coming into Finland from the south (Hackman 1905), and the finds from Raasepori Kroggårdsmalmen tarand graves featured prominently in these narratives during the later decades (see, e.g., Asplund 2008: 201-202; Jansson 2011: 124). Recent research has refined these interpretations, and it is now known that the genomes of modern Finns are a mixture of immigrants from different time periods, and that people have arrived in the Finnish region from many directions over the millennia (Salmela 2025). The tarand graves have been associated with movements of Proto-Finnic-speaking groups rather than ethnic "Finns" over the Baltic Sea (e.g, Lang 2020: 278 - 281). The later excavated tarand graves at Sauvo Korvala and chronologically comparable sites at Porvoo Pikku Linnamäki and Nakkila Penttala, are also archaeologically significant, as they contribute to the broader image of the Roman Period in Finland. Unfortunately, no usable DNA has been obtained from any of these burials.

IS POOR SKELETAL PRESERVATION AN ISSUE?

In Finland, the environmental conditions present a challenge for the scientific analyses of archaeological human remains. The characteristically acidic soils accelerate the decomposition of unburnt bone, often leaving little to no recoverable skeletal material (Moilanen 2021: 31–32; Taavitsainen 1997: 53). From the Stone Age, when inhumation was practised, only small fragments of teeth and enamel typically survive (Ahola et al. 2016). During the Bronze Age (c. 1500–500 BCE), cremation became the dominant burial custom and remained so until the Late Iron Age (around 1000 CE). As cremation destroys DNA (Hansen 2017), most burials from this long period are currently unsuitable for genetic studies. A few notable exceptions exist, such as the water burial of Leväluhta (c. 400–600 CE) in Western Finland (Lamnidis et al. 2018), where the exceptionally good preservation of human remains is attributed to the waterlogged conditions, and a limited number of Early Iron Age (c. 500 BCE–400 CE) cairns and tarand graves, from which some unburned skeletal elements have survived. Some of the samples in our dataset could even originate from incomplete cremations, as they come from find contexts where cremated bones were also present (for example, Kokemäki Leikkimäki, Kuopio Kuusikkolahdenniemi, Pori Leppänen, and Uusikaarlepyy Helgobacken).

Inhumation burials began to increase from the Merovingian Period (c. 600–800 CE) and Viking Age (c. 800–1050 CE) onward in South-Western Finland, and in other regions by the Early Medieval period (c. 1050–1250 CE) (Hiekkanen 2010). The Early Medieval inhumation burials generally represent the oldest broadly available skeletal material for scientific analyses in Finland, although the preservation varies greatly even within a single site (Fig. 3). For example, at the Valkeakoski Toppolanmäki cemetery, grave 3/1937 contained a well-preserved skeleton buried without grave-goods or a coffin, whereas the adjacent grave 2/1936 contained a completely decomposed individual with only a phalanx preserved inside a finger ring. (Moilanen 2021: 32). Interestingly, soil analysis from grave 3/1937 has revealed the presence of Sphagnum moss (Moilanen et al. 2022a), whose complex carbohydrates are known to inhibit microbial decomposition (Børsheim et al. 2001; Hájek et al. 2010). This highlights the fact that while soil acidity is a major factor in bone preservation, it is not the only one. Studies on taphonomy and human remains have shown that contextual variables

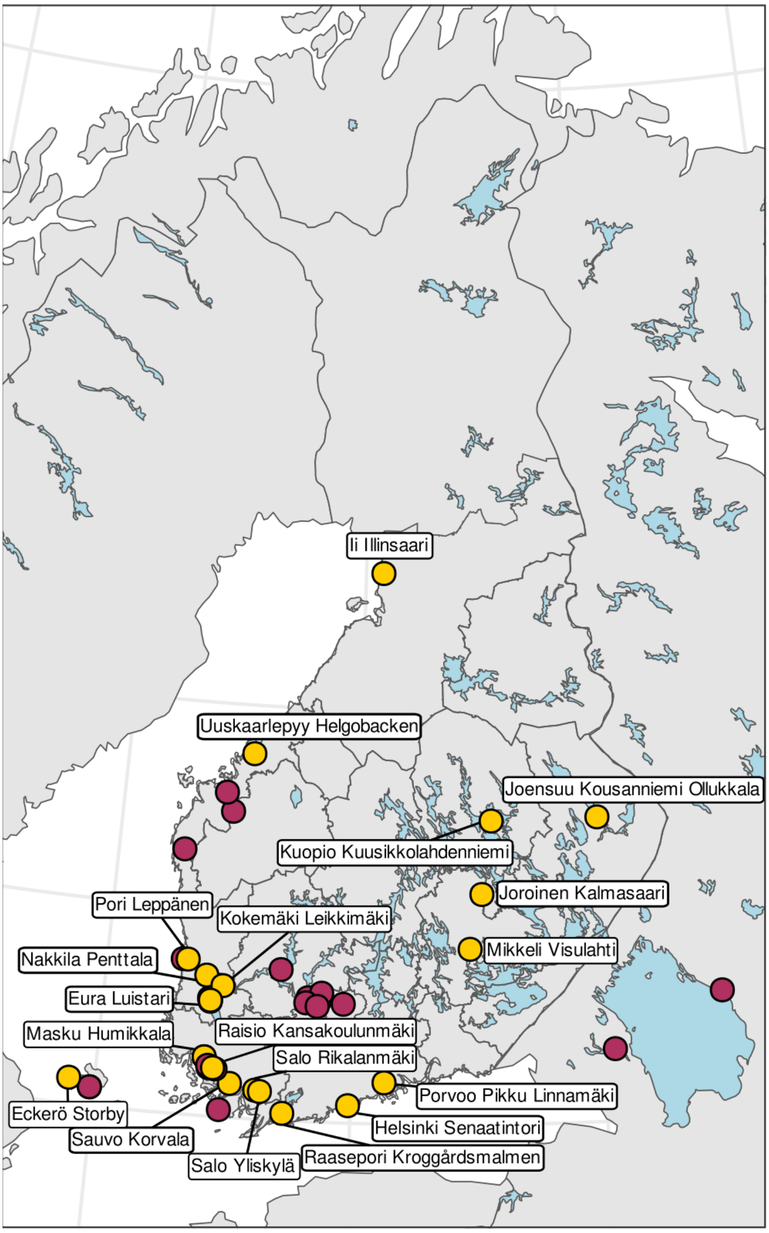

Figure 1. A map showing the locations of sites where unsuccessful samples are reported in this article. Sites discussed in the text are indicated with labels and highlighted with yellow markers, while other sites listed in Table 1 are marked in red.

and post-burial conditions can either slow down or accelerate the decay of organic material, including DNA. Among the most influential are pH, microstructure, and geochemistry of the soil, and microbial activity in the grave (Gordon & Buikstra 1981; Kibblewhite et al. 2015). Burial depth and the presence of containers, textiles or other organic materials can create microenvironments that further affect decomposition (Dent et al. 2004; Nord et al. 2005; Stojanowski et al. 2002; Emmons et al. 2020). Seasonal conditions at the time of burial also matter: colder and drier climates and weather conditions tend to delay decomposition (Mann et al. 1990; Roberts & Dabbs 2015), while elevated body temperature before death due to fever or sepsis may accelerate it (Hayman & Oxenham 2016).

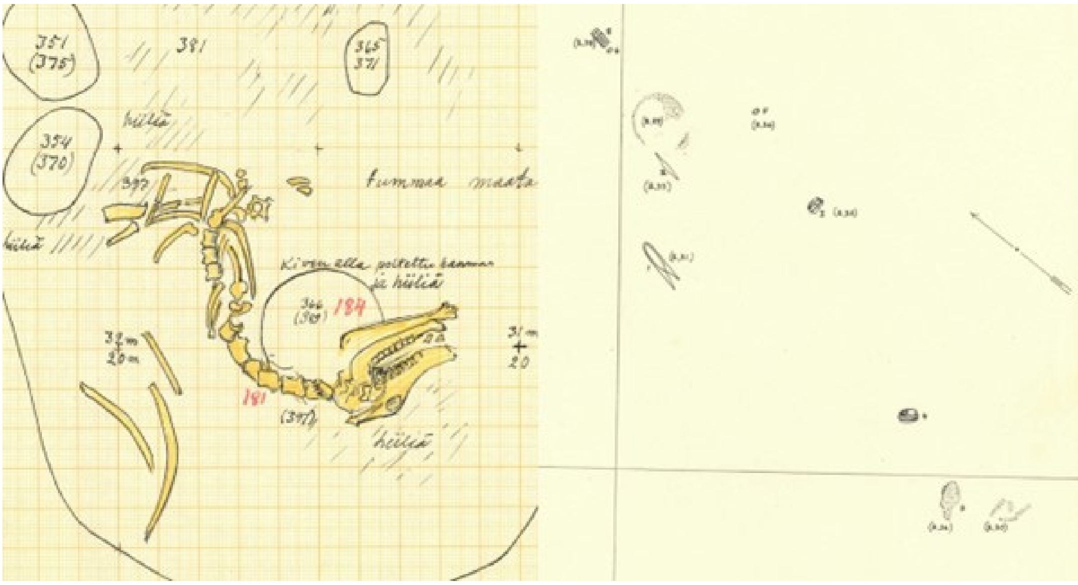

Figure 2. The "sacrificial ox of Mikkeli" on the left, and a Merovingian Period burial 7/1934 at the Köyliö Köyliönsaari (Kjulo Kjuloholm) cemetery on the right. In the documentation materials, the animal grave appears relatively well-preserved by Finnish standards (see also Taavitsainen 1990), while the Merovingian Period burial represents a more typical case in which only faint traces of decomposed bone are visible. Images: Jorma Leppäaho and Nils Cleve.

However, the visual condition of the bone does not automatically indicate whether or not DNA has been preserved. For example, at Tampere Vilusenharju, DNA has been successfully recovered from a tooth attached to a poorly preserved mandible, while no usable DNA was obtained from the petrous part of a well-preserved cranium in another grave (Nordfors et al. 2025a). It is noteworthy that even in geographical areas generally considered more favourable for bone preservation, such as certain parts of Åland, attempts to recover aDNA from relatively well-preserved remains have sometimes been unsuccessful.

PREDICTORS OF SUCCESSFUL DNA RECOVERY

Because our model treated DNA recovery as a binary outcome (success/failure), the results reflect the likelihood of obtaining any amount of analysable human DNA and do not take into account variation in data quality among successful samples. The strongest predictor for successful human DNA recovery was skeletal element: Petrous bones and teeth had substantially higher odds (OR: 65, 95% CI: 18–350 for petrous bones, OR: 6, 95% CI: 2–22 for teeth; Table S2) of successful human DNA recovery than other skeletal elements. These results are consistent with previous studies that have identified petrous bones and teeth as the most reliable sources of human aDNA (Damgaard et al. 2015, Hansen et al. 2017; Parker et al. 2020; Haarkötter et al. 2023). The odds ratios reported here may, however, be inflated by our sampling strategy: guided by previous studies, we selected petrous bones and teeth whenever they were available and only resorted to other skeletal elements when necessary. Thus, the extremely poor DNA preservation in elements other than petrous bones and teeth in our dataset may partly reflect the overall poor preservation of these burials.

In our model, sample age had a noticeable effect on DNA recovery: older samples were less likely to yield usable DNA. This is in line with DNA decay over time. In our dataset, library build had little effect on DNA recovery: single-stranded libraries showed a slight trend toward a

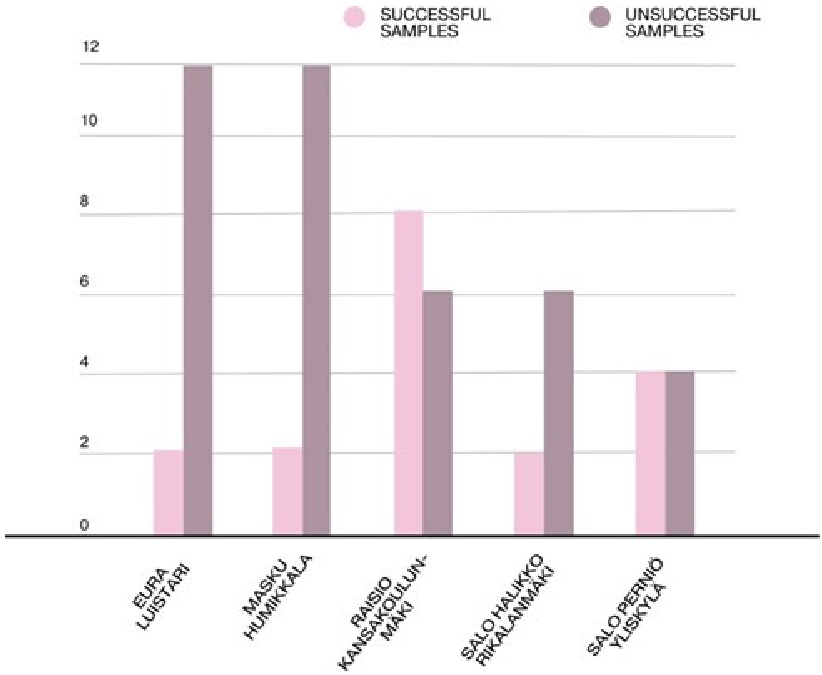

Figure 3. Number of unsuccessful and successful aDNA samples from selected Late Iron Age and Early Medieval sites in southwestern Finland. The outcomes present the variability of DNA preservation even within sites.

higher success rate, but this difference was not statistically significant. Notably, random site-specific factors accounted for approximately one-third of the variance in success rates, highlighting the role of depositional and environmental conditions in DNA preservation.

SAMPLING OUTCOMES BY SKELETAL ELEMENTS

The choice of skeletal element is widely recognised as one of the most critical factors in successful aDNA recovery. As stated above, the petrous part of the temporal bone is consistently identified as the most reliable source of endogenous aDNA, followed by dental root cementum. More recently, auditory ossicles have also shown potential despite their small size (Sirak et al. 2020). As noted above, our results support the previous findings (Fig. 4–6). By contrast, none of our samples taken from phalanges yielded usable DNA. Calcani, tali, and long bones have performed well in some previous studies (Emmons et al. 2020; Galob et al. 2024), but we have had no success with these bones. This likely reflects the overall poor preservation of Finnish burials, as we have only sampled these skeletal elements when no other elements have been available.

Some of the failed samples in our dataset (Table 1, SI) come from extremely poorly preserved inhumation burials, where skeletal material has survived only in association with metal objects (Fig. 7). These examples include arm and finger bones preserved inside arm and finger rings (e.g., Eura Käräjämäki-Osmanmäki, Luistari, and Pappilanmäki, Porvoo Pikkulinnamäki, Karjaa Kroggårdsmalmen, Sauvo Korvala). None of these samples have yielded human DNA.

The forensic study by Emmons et al. (2020) found that DNA preservation varies between different bones within the same individual and even within the same bone. Our dataset provides some support for this observation. For example, a humerus from grave 2 at Ii Illinsaari (sample ILS003 in Table 1) did not yield human DNA, whereas a tooth taken from the same individual

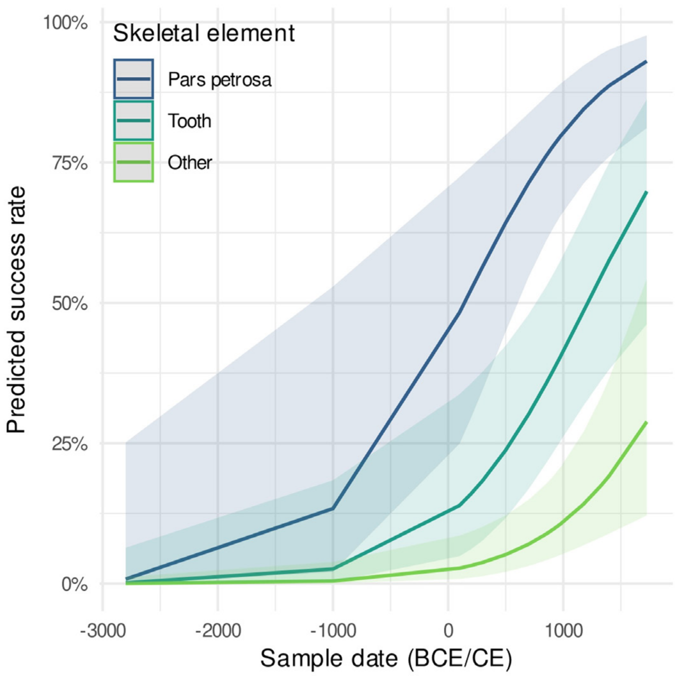

Figure 4. Predicted success rates of human DNA recovery for petrous bones, teeth, and other skeletal elements over a range of sample ages based on a generalised linear mixed model. Predicted probabilities are averaged over sites and library types; probabilities for a specific site or library type would be lower, particularly at older ages.

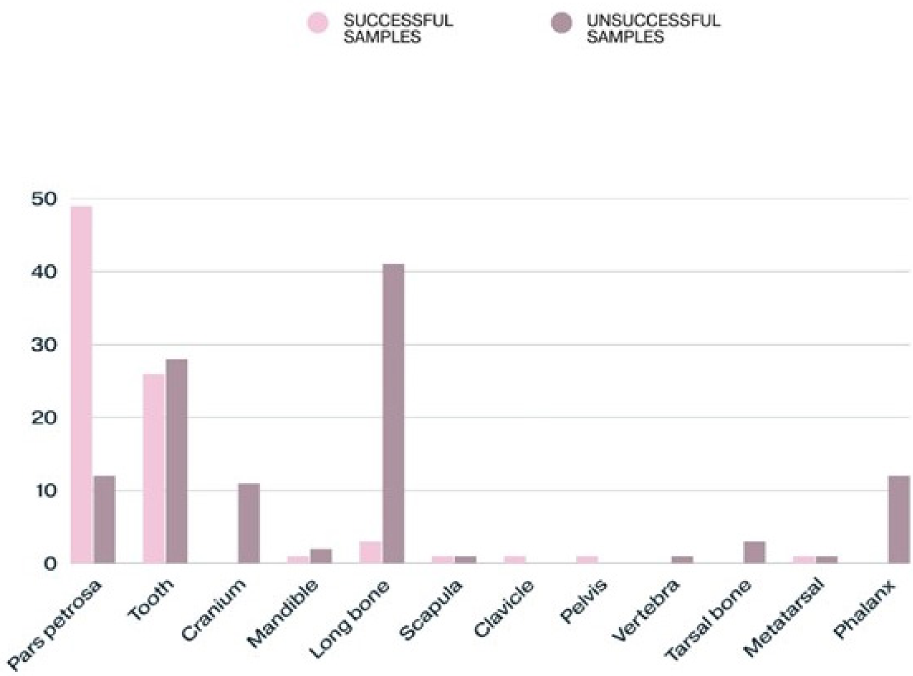

Figure 5. The sampled skeletal elements confirm findings from previous studies: the petrous part of the temporal bone is the most reliable element for DNA recovery. Samples from crania, phalanges, vertebrae and tarsal bones did not yield any DNA.

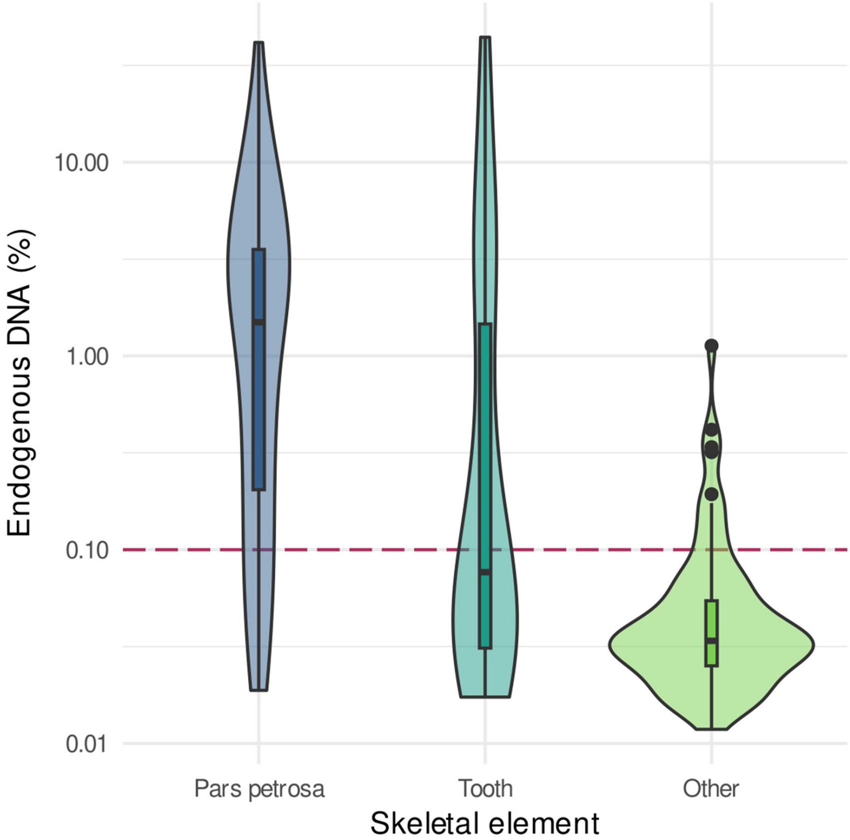

Figure 6. Endogenous DNA in different skeletal elements. Violin and box plots show the distribution of endogenous DNA percentage in pars petrosa, teeth, and other skeletal elements. The dashed line shows a common cut-off of endogenous DNA; samples with lower endogenous DNA are usually considered too poorly preserved to analyse further. The y-axis is on a log10 scale.

did. However, there are several examples in our dataset where sampling different bones from the same individual or burial context did not improve the results. For example, two different molars of an individual from grave 12/2014 at Illinsaari did not yield human DNA. Both a femur (RK3003) and a tooth (RK3004) from the same grave at Raisio Kansakoulunmäki did not yield usable human DNA. Similarly, two separate phalanges (MEL001) and a tooth (MEL003) from Eckerö Storby, Åland – all three possibly belonging to the same individual – were sampled without success. The same applies to the "Eura matron", from whom both *pars petrosa* and a tooth were sampled, but neither yielded DNA. Thus, occasionally, DNA has not been preserved even in the anatomically most favourable elements (Fig. 8).

TEMPORAL VARIATION

Based on archaeological contexts, some of the oldest remains from mainland Finland in our dataset are thought to derive from Bronze Age cremations (Table 1, SI), although the possibility of later secondary burials should also be considered. Several samples have been taken from bones deriving from Early Iron Age contexts, such as Roman and Migration Period (c. 1–600 CE) inhumation burials. These remains come from various burial types, and they represent some of the oldest Iron Age inhumations in Finland, but the success rates have been fairly low (Table 2). To date, only two attempts to recover DNA from Merovingian Period inhumation burials (c. 600–800 CE) in Finland have

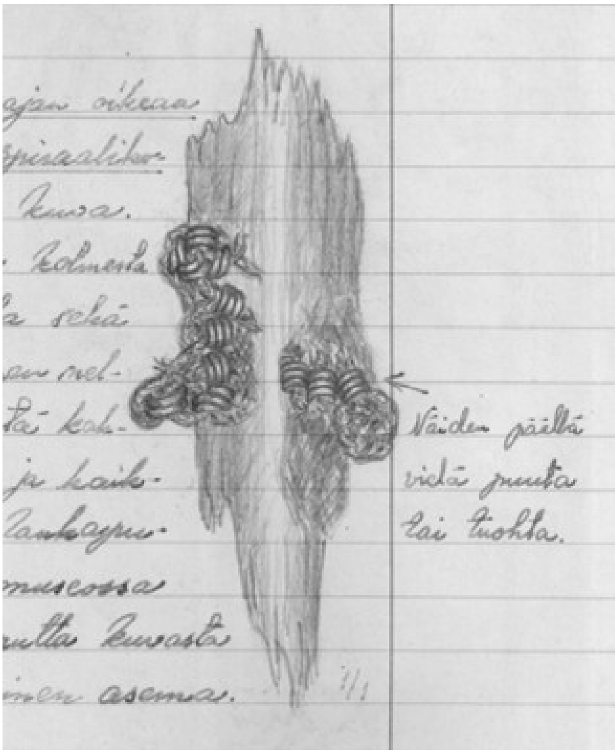

Figure 7. A drawing of bronze spirals and a bone fragment preserved beneath them in grave 2/1965 at Eura Yli-Nuoranne. Sample YLI001 was taken from the bone. In many Finnish cases, these kinds of fragments may be the only surviving bone material in an Iron Age grave. In unfurnished burials, the preservation may be even worse, although this varies even within sites. Image: Object catalogue KM 16950, Pirkko-Liisa Lehtosalo-Hilander.

Figure 8. DNA is not always well preserved even in anatomically favourable elements. Examples of sampled skeletal elements that did not yield DNA. Top row: petrous parts of the temporal bone from Eura Luistari (LUI034 and LUI033) and Nakkila Penttala (NAP001, on the right). Bottom row: a tooth from Helsinki Senaatintori (HKI006) and a talus from Salo (Perniö) Yliskylä (PYL005). Photos: K. Majander (LUI034, LUI033, NAP001, HKI006) and N.-J. Saari (PYL005).

Table 2. Samples from the Early Iron Age had a lower success rate compared to the Late Iron Age and Early Medieval samples, and the highest success rates were seen in the youngest samples. However, the chronologically younger samples, which generally yield more DNA may also have spent less time in museum storage, as the excavations of post-medieval sites in Finland have only become relatively common since the 1980s and 1990s.

Dating	**–500 BCE**	**Early Iron Age (500 BCE–700 CE)**	**Late Iron Age (700–1100 CE)**	**Early Medieval (1100–1250 CE)**	**Medieval and Post-Medieval (1250 CE –)**
Successful samples	-	9	10	50	13
Unsuccessful samples	5	19	7	40	5
Success rate %	0%	32.1%	58.8%	55.6%	72.2%

been successful.[1] This is reflected in our GLMM model, which shows a rather rapid drop in the predicted DNA recovery rate with time. However, even though DNA degrades progressively over time, there is substantial variation in DNA preservation among samples with similar chronological age (Thomas 1993: 4). Notably, even though none of the samples from the Early Iron Age tarand graves have yielded DNA, some contemporaneous samples from coastal cairns, such as Raahe Tervakangas and Vöyri Latjineliden, have produced usable data which is now under analysis for forthcoming publications. These differences are likely influenced more by regional and local preservation conditions, as well as the sampled skeletal element, than by the age of the remains.

Some previous studies have even reported better success on older samples compared to younger samples (Leney 2006; Tourunen & Niemi 2011: 35–36). The same has been observed at Pälkäne Rauniokirkko, where some 13th-century samples produced usable DNA, whereas one post-medieval burial did not (Nordfors et al. 2025a). Our dataset also includes other post-medieval cases in which no usable DNA was recovered from the samples (for example, Helsinki Senaatintori, Joroinen Kalmasaari, or the Orthodox cemetery at Joensuu Kousanniemi Ollukkala). The sampled skeletal elements from Senaatintori and Kalmasaari were teeth, suggesting that the lack of DNA preservation in these particular cases is strongly affected by burial-specific factors.

FUTURE PROSPECTS

Researchers and collection managers are frequently faced with the question of whether to sample human remains now or preserve the material until new analytical techniques are available. Because future methodological breakthroughs – much like those seen in the rapid development of aDNA research – cannot be predicted, careful preservation and curation of human remains are essential for future research. However, waiting is not always the best option, because DNA decay does not stop when the archaeological material is excavated and moved into a museum collection. Previous studies have shown that DNA may be better preserved in recently excavated materials (Eriksen et al. 2025; Nordfors et al. 2025a). In our dataset, long-term storage may have contributed to DNA degradation in some of the failed samples, as many of them were excavated decades ago, and some over a century ago (e.g., Appelgren-Kivalo 1907 [the description of excavation finds from Perniö in 1893], Ailio 1912; Pälsi 1925; Hackman 1930). However, some samples still yielded usable DNA despite having been curated in museum collections for over 130 years (e.g., KM 2487 and KM 2503, accessioned in 1887). This issue has received relatively little attention in aDNA studies, but it nevertheless raises questions about long-term preservation environments in museums. Given the broad scientific and cultural value of human remains, attention to storage conditions and practices is crucial for ensuring their value for the future.

In most cases, it is unlikely that the same unsuccessful samples presented here would yield usable aDNA in the future without significant methodological advances. The primary issue is not technical, but biological: When an organism dies, its DNA begins to degrade into increasingly shorter fragments until it is entirely gone. This degradation is driven by a range of taphonomic and environmental factors. Understanding these factors more precisely may require further research, which could be essential for reviewing sampling strategies in the future.

Our analyses have measured the preservation of human DNA, and although it likely reflects the overall DNA preservation in the sample, it remains theoretically possible that pathogen DNA could have survived even if human DNA has not. However, screening for ancient pathogen DNA can also be recommended, as it can provide information on the prevalence and impact of past diseases, while helping to clarify the circumstances and motives behind certain burial practices. Particularly in the cases of double or mass burials, it is generally advisable to sample more than one individual, if not all, as this would allow for the investigation of kinship relations and potential shared causes of death among the buried, provided DNA preservation is adequate (c.f. Haak et al. 2008; Schroeder et al. 2019).

In cases where DNA preservation is poor, valuable information can still be obtained with other methods. For example, paleoproteomics offers a promising alternative for aDNA analysis by providing information on the health and biological sex of the individual (Hendy 2021; Warinner et al. 2022). Likewise, isotopic analyses can illuminate aspects of past diets and mobility even for individuals whose DNA has not been preserved. For example, the teeth of the "Eura matron" have been successfully analysed with isotopic methods (Danielisová et al. 2025) despite unsuccessful DNA extraction. As analytical techniques continue to evolve, the range of information that can be derived from previously unsuccessfully sampled materials expands. This progress broadens the ways in which we can study human lives in the past and reduces reliance on a single methodological approach. In most cases, combining multiple lines of evidence can be the most fruitful way to carry out research on the same material, as different methods offer access to different types of information and can compensate for each other's limitations.

CONCLUSIONS

This study highlights the anatomical, temporal and environmental factors affecting ancient human DNA preservation in archaeological remains found in Finland. Despite the challenging preservation conditions caused by acidic soils, high microbial activity, and frequent cremation practices, usable aDNA has been recovered from various contexts. Our results reaffirm that the petrous part of the temporal bone remains the most reliable skeletal element for aDNA studies, followed by teeth, and that changes of DNA preservation in human remains decrease over time. Our examples also show that DNA survival in individual sites or burials can be highly unpredictable, and macroscopically well-preserved bone does not always correlate with molecular preservation. Temporal and regional patterns in DNA preservation were also observed. Chronologically younger samples, particularly from the Medieval and Post-Medieval periods, had higher success rates than earlier material, but these patterns may also reflect shorter museum storage times. Notably, some Early Iron Age coastal cairns produced usable DNA, whereas all tarand grave samples failed, suggesting that local conditions or burial practices may play a greater role than burial chronology alone. Given the irreversible nature of destructive sampling and the uncertainty of future technological advances, it is essential to balance research needs with the careful curation of human remains. Continued documentation, transparency, and publication of both successful and failed results will support more informed decision-making and promote responsible use of archaeological resources.

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Endnotes

1 Additionally, DNA has been successfully obtained from the Migration and Merovingian-Period site of Levänluhta, where unburned individuals were deposited in water (Lamnidis et al. 2018; Översti et al. 2019).