

## Genetic Analysis of Birnirk Inuit from the Alaskan North Slope

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**ABSTRACT.** Archaeological evidence indicates that Birnirk peoples (AD 650–1300) are the proposed genetic ancestors of the Thule Inuit (AD 950–1400) and are potentially an intermediary population between the Thule Inuit and earlier Old Bering Sea people (AD 1–1000). We sequenced the first hypervariable region of the mitochondrial DNA of 22 clearly associated Birnirk individuals from the Piġniq (Birnirk), Kugok, Kugusugaruk, and Nunavak sites on the North Slope of Alaska. Haplotypes A2a, A2a1, A2a3, A2b1, and D4b1a2a1a were identified in this population, demonstrating an expansion of Birnirk maternal genetic diversity. Maternal lineages from these individuals were evaluated with other past and contemporary Inuit populations from the Chukotka Peninsula to eastern Greenland. Our findings confirm Birnirk Inuit as probable maternal ancestors to Thule Inuit and may be among the first peoples possessing these lineages to have moved into the western North American Arctic from the Bering Strait region.

**Key words:** Birnirk; Thule; Inuit; Arctic; ancient DNA

**RÉSUMÉ.** Selon des preuves archéologiques, les Birnirks (650 à 1300 A.D.) sont les ancêtres génétiques proposés des Inuits thuléens (950 à 1400 A.D.) et pourraient représenter une population intermédiaire entre les Inuits thuléens et un peuple antérieur du Vieux Béring (1 à 1000 A.D.). Nous avons séquencé la première région hypervariable de l'ADN mitochondrial de 22 individus se rapportant manifestement aux Birnirks en provenance des sites Piġniq (Birnirk), Kugok, Kugusugaruk et Nunavak sur le versant nord de l'Alaska. Les haplotypes A2a, A2a1, A2a3, A2b1 et D4b1a2a1a ont été identifiés au sein de cette population, ce qui démontre une expansion de la diversité génétique maternelle des Birnirks. Les lignées maternelles de ces individus ont été évaluées par rapport à d'autres populations anciennes et contemporaines d'Inuits, allant de la péninsule des Tchouktches jusqu'à l'est du Groenland. Nos constatations permettent de confirmer que les Inuits birnikiens sont les ancêtres maternels probables des Inuits thuléens et qu'ils pourraient figurer parmi les premiers peuples à posséder ces lignées à s'être installés dans l'Arctique nord-américain occidental en provenance de la région du détroit de Béring.

**Mots clés :** Birnirk; Thulé; Inuit; Arctique; ADN ancien

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### INTRODUCTION

The relationship of Thule Inuit to contemporary Inuit, which includes Inuit in Canada and Greenland, Iñupiat, Inuvialuit, Alaskan Yup'ik, Siberian Yupik, Cup'ik, and Sugpiat, and their cultural predecessors in the Bering Strait region, is genetically understudied. Many archaeologists hypothesize Birnirk people as the cultural ancestors of Thule Inuit (De Laguna, 1947; Collins, 1964; Stanford, 1976; Morrison, 2001), often with significant Punuk

cultural influences (Collins, 1937; Anderson, 1984; Bandi and Blumer, 2002; Dumond, 2002; Jensen, 2009; Mason, 2016a). Alternative hypotheses propose Alaskan Ipiutak or Norton as potential contributors to Thule in west and southwest Alaska (De Laguna, 1947; Larsen and Rainey, 1948; Collins, 1964; Shaw, 1982, 1998; Fitzhugh, 1988; Griffin, 2004; Mason and Friesen, 2017). Genetic analysis of proposed direct Thule ancestors is limited to five Birnirk individuals from the Paipelghak site on the Chukotka Peninsula (Raghavan et al., 2014). These individuals exhibit

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low maternal genetic diversity compared to other Inuit populations (Tackney et al., 2019). It is unclear if this low mitochondrial diversity represents the full extent of the Birnirk maternal gene pool or if other Inuit lineages have yet to be documented in Birnirk populations. To address this question, we analyzed individuals from four Birnirk sites on the Alaskan North Slope. If this low diversity persists despite a larger sample size, Birnirk populations are an unlikely ancestor of all Thule Inuit and potentially represent a small subset of previous populations, such as the Old Bering Sea people. If the other Inuit lineages are present in the Birnirk populations, it is likely that Birnirk populations represent an intermediary between earlier Old Bering Sea populations and later Thule Inuit populations.

The Inuit tradition consists of several archaeologically defined cultures: Okvik, Old Bering Sea, Punuk, Birnirk, Thule, and contemporary Inuit from the Chukotka Peninsula to eastern Greenland. Based on archaeological evidence, the Inuit tradition first appears in the archaeological record around 250 BC, with the rise of the Okvik and Old Bering Sea material cultures on the shores of the Chukotka Peninsula and St. Lawrence Island (Geist and Rainey, 1936; Collins, 1937; Arutiunov et al., 1964; Bronshtein and Dneprovsky, 2002; Mason, 2016b). The Birnirk and Punuk cultures likely developed contemporaneously from the Old Bering Sea culture (Mason, 2016a). People associated with Punuk material culture (AD 800–1100) occupied St. Lawrence Island and the northern coastlines of the Bering Sea (Collins, 1937; Bandi and Blumer, 2002; Mason, 2009, 2016a). Birnirk people occupied the margins of the Chukchi Sea (Fig. 1A) from approximately AD 650–1300 (Collins, 1937; Mason, 2016a). Birnirk and Punuk peoples then expanded along the shores of northwest Alaska (Mason, 2009; Friesen, 2013), where it has been proposed that the Thule Inuit developed from Birnirk populations (Morrison, 2001; Mason, 2016a).

Contemporary and past Inuit populations appear to carry specific mitochondrial DNA (mtDNA) haplotypes, or named combinations of genetic variants across a chromosome. These represent distinct maternal lineages and provide information on ancestry, maternal relatedness, and population gene flow. These mtDNA haplotypes, A2a, A2b1, and D4b1a2a1a, are themselves part of a subset (with D2a, D2b, and D4b1a2a1b) that can be referred to as “Beringian specific” given their relatively limited geographic occurrence compared to other Native American haplotypes (Helgason et al., 2006; Raghavan et al., 2014; Raff et al., 2015; Lopopolo et al., 2016; Flegontov et al., 2019; Tackney et al., 2019).

Genetic analyses of past individuals culturally associated with the Inuit tradition but not affiliated with Thule are limited. Thirty-three individuals from the Uelen and Ekven (cal. 125 BC to AD 1485) sites on the Chukotka Peninsula have been genome-wide captured. Individuals from these cemeteries exhibited the Inuit-associated mitochondrial haplotypes mentioned above (A2a, A2b1, and D4b1a2a1a).

Genome-wide data from these individuals indicated a close relationship with contemporary Iñupiat from the Alaskan North Slope, Inuit from Greenland, and Siberian Yupik from along the coast of the Chukchi Peninsula. A large portion of their ancestry (69%) was derived from Paleo-Siberians (represented by Kolyma 1), and there is evidence of a back migration of Native Americans (represented by Anzick) across the Bering Sea post-dating the Ancient Beringian population (represented by USR1) (Flegontov et al., 2019; Sikora et al., 2019). Unfortunately, burials and radiocarbon dates at these sites are associated with multiple cultures, including Old Bering Sea, Okvik, Birnirk, and Punuk, making specific cultural and genetic affiliations difficult to interpret (Arutiunov et al., 1964; Bronshtein and Dneprovsky, 2002). Five individuals from the Birnirk site of Paipelghak have also been mitogenome genotyped. All were classified within haplotype A2a and deemed closely related to Thule and contemporary Canadian and Greenlandic Inuit sequences (Raghavan et al., 2014). Like the Uelen and Ekven sites, Paipelghak exhibits potential confounding issues due to a complex depositional history, with evidence of Old Bering Sea, Punuk, and Birnirk affiliations (Dneprovsky, 2006). No clearly affiliated Punuk human remains have been analyzed.

The Thule Inuit (ca. AD 950–1400) migrated eastward and their archaeological sites are dispersed along the Alaskan, Canadian, and Greenlandic coastlines. Thule Inuit possessed mitochondrial haplotypes A2a, A2b1, and D4b1a2a1a (Raghavan et al., 2014; Tackney et al., 2019). Mitochondrial DNA from contemporary Inuit individuals from the Alaskan North Slope (Iñupiat) indicate a continuation of these same haplotypes. On the North Slope, a majority of individuals (90.5%) are categorized within haplogroup A (haplotype variations of A2 “root,” A2a, A2a3, and A2b1), while a minority (8.0%) possess haplotype D4b1a2a1a (Raff et al., 2015). Similar results (a majority A2a and A2b1 and a minority of D4b1a2a1a) are reported in contemporary Inuit populations across Canada and Greenland (Saillard et al., 2000; Helgason et al., 2006; Gilbert et al., 2008; Lopopolo et al., 2016).

The genetic relationship of populations ancestral to the Thule Inuit remains unclear. In this study, we attempt to sequence the first hypervariable region (HVR-1) of the mitogenome, as it is sufficient to identify the haplotypes commonly found in Inuit populations, from 38 individuals culturally associated with Birnirk. These individuals originated from four Birnirk archaeological sites on the North Slope of Alaska: Kugusugaruk, Nunavak, Kugok, and Piñiq (the Birnirk type site) (Ford, 1959) (Fig. 1B). As a proposed location of archaeological transition from the Birnirk to Thule Inuit cultures and hypothesized place of origin for the Thule Inuit migration (Taylor, 1963; Morrison, 2001; Jensen, 2009; Mason, 2016a; Friesen et al., 2019), the Alaskan North Slope presents a unique opportunity to test for genetic continuity between Birnirk, Thule, and contemporary Inuit populations.

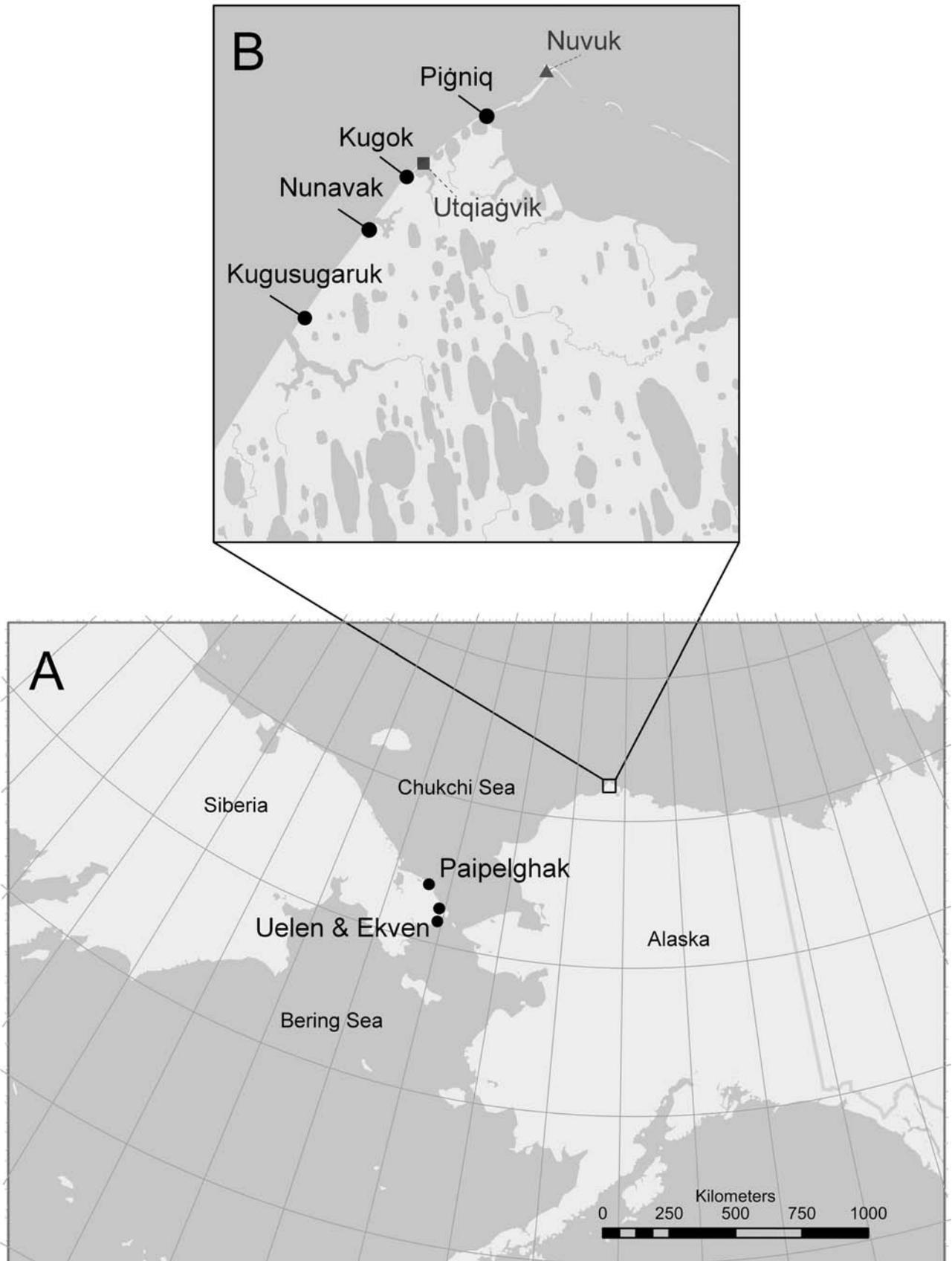


FIG. 1. A. Archaeological sites mentioned in text. Sites with sequenced human material (bone, teeth, or hair) shown as black circles. B. Birnirk sites included in this study shown in black circles. The Thule cemetery at Nuvuk shown in a grey triangle, and the contemporary community of Utqiagvik, Alaska, shown in a grey square.

## METHODS AND ANALYSES

*Consultation and Sampling*

This project was organized in collaboration with the Native Village of Utqiaġvik. We obtained written permission from the Native Village of Utqiaġvik and the Iñupiat History, Language and Culture department of the North Slope Borough to study the collection of Birnirk human remains from sites near the village of Utqiaġvik curated at the Smithsonian National Museum of Natural History (Hollinger et al., 2004). A subset of 38 Birnirk individuals was selected for ancient DNA (aDNA) extraction and sequencing. Individuals were chosen to proportionally represent each site and burial mound. We also assessed the quality and availability of contextual information.

*Extraction*

Sample preparation prior to extraction included surface bleaching, physical removal of the external surface of bone with a Dremel bit, and reduction of 80–150 mg of prepared bone to powder. The bone powder was transferred to a 1.5 mL LoBind tube. Digestion buffer containing 1959  $\mu$ L of 0.5 M EDTA (Sigma 03690), 25  $\mu$ L of 250  $\mu$ g/ml Proteinase K (Sigma P2308), and 16  $\mu$ L of 40 mM DTT (Sigma D9779) per sample was prepared. A double digestion was performed (55°C 1 hour, 37°C overnight) and the supernatant was concentrated in Amicon Ultra-4 30 kDa tubes. The concentrate was silica column cleaned and eluted in 60–70  $\mu$ L of TE-4+Tween-20 (Damgaard et al., 2015; Gamba et al., 2016; Rohland et al., 2018).

*Amplification*

Extractions were amplified in a dedicated PCR hood in the cleanroom (see below) using 50  $\mu$ L reactions containing variable microliters of Nuclease Free RT-PCR water (VWR, 490002-158), 5  $\mu$ L of 10 $\times$  PCR buffer, variable microliters of 25 mM MgCl<sub>2</sub> (ABI, 4311806), 4  $\mu$ L of 12.5 mM GeneAmp dNTP blend w/UTP (ABI, N8080270), 0.5  $\mu$ L UltraPure BSA (AM2618, ABI), 0.5  $\mu$ L of AmpliTaq Gold with Gold Buffer, and 0.5  $\mu$ L of 20  $\mu$ M for forward and reverse primers Tack\_HVR1\_P1F, Tack\_HVR1\_P1Rc, Tack\_HVR1\_P2Fb, Tack\_HVR1\_P2R, Tack\_HVR1\_P3F, Tack\_HVR1\_P3R, HVR1Car\_P1F, and HVR1Car\_P1Rb (Raff et al., 2010; Tackney et al., 2019) for all individuals. These four fragments were utilized to provide coverage between nucleotide positions 16043–16277 and 16288–16402 of the human HVR-1. Primers HVR1Car\_P1 and Tack\_HVR1\_P2 occasionally failed to amplify the corresponding mtDNA fragments. When possible, 0.5  $\mu$ L of 20  $\mu$ M of primers Unk\_HVR1\_P2F, Unk\_HVR1\_P2R, Unk\_HVR1\_P3F, and Unk\_HVR1\_P3Ra were utilized to account for missing coverage between nucleotide positions 16162 and 16182 (this study; Table 1). The template was 2

TABLE 1. Oligonucleotides first reported here. All other primers were previously published in Raff et al. (2010) and Tackney et al. (2019).

Primer ID	rCRS starting np	5'-3' Sequence
Unk_HVR1_P2F	16,133	CCATAAACTACTTGACCACCT
Unk_HVR1_P2R	16,232	GAGTTGCAGTTGATGTGTG
Unk_HVR1_P3F	16,244	GCAACTCCAAAGCCACCC
Unk_HVR1_P3Ra	16,394	GGAGGATGGTGGTCAAGG

$\mu$ L of extract DNA, extraction blank DNA, or PCR blank (water). Reagents and the number of cycles (between 40 and 45) were adjusted as needed for successful amplification. Reaction products were visualized on agarose gels and amplicons were sequenced by Genewiz.

*Contamination and Quality Control*

DNA extractions and PCR set-ups were conducted in Airclean AC600 ductless chemical workstations housed in separate cleanrooms of the KU Ancient DNA Research Facility, University of Kansas, Lawrence, Kansas. This facility is accessed exclusively by trained researchers and equipped with ceiling and hood UV lighting, positive room air pressure, and HEPA-filtered ventilation. Researchers are required to wear full body “Tyvek” suits as well as gloves, boots, sleeve covers, hairnets, facemasks, and respirators while in the laboratory, and they are required to bleach their entire suit prior to entering the aDNA lab. All reagents are certified DNA-free and are distributed via aerosol-resistant filter tips. Tubes are irradiated under UV light for five minutes prior to use. Negative extraction and PCR controls are included in each experiment. In addition, gloves are sterilized with bleach wipes frequently. Amplification is conducted in thermocyclers located in the KU Anthropological Genetics Research Facility, and workflow between the two facilities is unidirectional each day.

*Verification of Genetic Results*

A minimum of two independent extractions were performed for each individual in this study. Each sequence was confirmed through separate extractions and subsequent amplifications. None of the HVR-1 sequences reported here matched any of the laboratory researchers.

*Statistical Analyses*

mtDNA data from the HVR-1 of the control region were sequenced and analyzed to identify mitolineages. Sequencher version 5.4.6 (Gene Codes Corporation, Ann Arbor, Michigan) was used to align and manually correct the sequences. Mutations were noted when compared to the revised Cambridge Reference Sequence (rCRS) (Andrews et al., 1999); these mutations were used to determine corresponding haplotypes using Phylotree (van Oven

and Kayser, 2009). Summary statistical data, including nucleotide and haplotype diversity, the mean number pairwise differences, and population pairwise  $F_{st}$  statistics were calculated using sequence data in Arlequin 3.5.2.2 (Excoffier and Lischer, 2010). A principal component analysis (PCA) was completed based on haplotype frequencies using the package “adeget” (Jombart, 2008) in RStudio version 1.1.453.

Comparative genetic and genomic data were collected from all known studies of Inuit populations across the Siberian and North American Arctic. To avoid skewing the Alaskan data for the PCA, precontact Nunalleq individuals (Raghavan et al., 2014) were separated into their own population because of an unusually high A2a frequency. Individuals in the comparative dataset were removed if their corresponding haplotype could not be specified beyond the A or D haplogroups (Raghavan et al., 2014). Additionally, individuals classified as having A2a sub-haplotypes (such as A2a2, A2a3, etc.) were recategorized within the A2a haplotype for the purpose of the haplotype frequency analysis. Sequence data were limited to studies with published HVR-1 sequences (and not just genotypes) and individuals carrying single nucleotide polymorphisms (SNPs) between nucleotide positions 16043–16277 and 16288–16402.

## RESULTS

Twenty-two Birnirk individuals from the Alaskan North Slope yielded contamination-free HVR-1 sequences. This number represents an amplification success rate of 57.9%. Table 2 displays the HVR-1 SNPs present in the covered fragments relative to the rCRS (NC\_012920; Andrews et al., 1999) between nucleotide positions 16043–16277 and 16288–16402, unless otherwise specified in the “Missing coverage” column. One individual (P365894-0) included in the analyses was unable to be fully replicated following failed amplification attempts for second and third extractions. However this individual was left in the analysis because the determined haplotype was consistent with expectations, and they came from Kugok, a site with few individuals. The final subset of Birnirk individuals analyzed included two individuals from the Pigniq site, three each from Kugok and Nunavak, and 14 from the Kugusugaruk cemetery. These sites are classified as Birnirk based on harpoon heads and other diagnostic artifacts spanning early to late Birnirk typologies (Ford, 1959).

Human bone elements from 19 individuals sampled for aDNA analysis were also prepared (Beaumont et al., 2010) and directly radiocarbon dated (Table 3) at the Keck Carbon Cycle AMS Laboratory, University of California Irvine. Conventional radiocarbon ages (Stuiver and Polach, 1977) and stable isotope values are presented in Table 3, quoted according to the international standard set at the Trondheim Convention (Stuiver, 1986). Following the linear equation for dietary estimates presented in Arneborg et al. (1999),

we estimated the percentage of the diet (with an uncertainty of 10%) for these individuals using the context appropriate  $\delta^{13}C$  end members for Point Barrow’s late precontact human populations provided in Krus et al. (2019). Following Krus et al. (2019), we used  $-13.8\text{‰}$  and  $-18.6\text{‰}$  as the end members for the  $\delta^{13}C$  values, where  $-18.6\text{‰}$  was the equivalent of 100% terrestrial and  $-13.8\text{‰}$  was equal to 100% marine. The measurements were then corrected for calibration using OxCal and mixing the terrestrial and marine calibration curves of Reimer et al. (2020) and Heaton et al. (2020) based on the calculated percentages for marine diet. Local reservoir effects from marine carbon were corrected with the  $\Delta R$  correction  $278 \pm 94$  years, which is the weighted-mean  $\Delta R$  correction estimated in Krus et al. (2019) for Point Barrow’s late precontact human populations calculated with the 2020 calibration curves (Heaton et al., 2020; Reimer et al., 2020). Calibrations are presented in Table 3 as both 95.4% and 68.3% confidence intervals with the end points rounded outwards to 10 years.

A total of six distinct haplotypes were identified in the North Slope Birnirk population, resulting in a haplotype diversity value of  $0.78 \pm 0.05$  and mean pairwise difference, or average number of differing nucleotide positions, of  $2.62 \pm 1.45$  (Table 4). All individuals were classified within mitochondrial lineages A2a, A2b1, and D4b1a2a1a, with some individuals further classified to clade haplotypes or sub-haplotypes, A2a1 and A2a3. The D2a lineage, commonly found in Paleo-Inuit, was not detected. Haplotype frequencies were 27.3% A2a, 9.1% A2a1, 4.5% A2a3, 40.9% A2b1, and 18.2% D4b1a2a1a. Figure 2 provides a detailed view of these frequencies by site. Pairwise  $F_{st}$  values from the sequence data (Table 5), which serve as measurement of population differentiation, indicate moderate to strong population structure between the four Birnirk sites (excluding Kugok-Kugusugaruk), though sample counts are low.

The North Slope Birnirk population can be placed in context with published maternal genetic data from Thule and contemporary Inuit of the North American Arctic. HVR-1 sequence data from Birnirk, Thule, and Iñupiat populations on the North Slope of Alaska (Raff et al., 2015; Tackney et al., 2019; this study) are compared in Table 6. Pairwise  $F_{st}$  values indicate minimal population substructure among groups in the region. Table 7 offers a broader comparison of available HVR-1 sequence data from known Inuit populations (minus those studies where only genotype data was collected). The North Slope Birnirk Inuit were a diverse population and this maternal variation appears to have held steady throughout time and across the Arctic. To broaden the comparison, we reverted to haplotype determinations in Table 8 and constructed a principal component analysis. The first principal component (comprising 74.2% of the variance) aligns with expectations that Inuit populations are closely maternally related. The second principal component shows the precontact Nunalleq and Siberian Birnirk from Paipelghak are distinguished for their lack of mtDNA diversity (all individuals from both



TABLE 3. AMS <sup>14</sup>C measurements from human bones obtained for this study.

Laboratory code	Site	Accession number	Element	Conventional <sup>14</sup> C age (BP)	δ <sup>13</sup> C (‰)	δ <sup>15</sup> N (‰)	Atomic C:N	Radiocarbon calibration (95.4% confidence)	Radiocarbon calibration (68.3% confidence)
UCIAMS-210684	Pigniq	P365905-0	Rib	1660 ± 15	-13.5	20.9	3.23	cal AD 850–1300	cal AD 980–1230
UCIAMS-210685	Pigniq	P365903-0	Patella	1720 ± 15	-12.5	20.3	3.23	cal AD 780–1250	cal AD 900–1160
UCIAMS-210686	Kugok	P365895-0	Talus	1780 ± 20	-12.9	20.0	3.38	cal AD 710–1190	cal AD 830–1100
UCIAMS-210687	Kugok	P365896-0	Patella	1730 ± 20	-13.4	20.8	3.36	cal AD 770–1250	cal AD 890–1150
UCIAMS-210688	Kugusugaruk	P381124-0	Clavicle	1715 ± 15	-13.1	21.5	3.29	cal AD 790–1260	cal AD 910–1170
UCIAMS-210689	Kugusugaruk	P381107-0	Vertebra	1700 ± 20	-14.1	20.7	3.40	cal AD 780–1260	cal AD 900–1160
UCIAMS-223308	Kugusugaruk	P381099-0	Talus	1735 ± 15	-13.4	21.4	3.19	cal AD 770–1240	cal AD 890–1160
UCIAMS-210690	Kugusugaruk	P381109-0	Clavicle	1700 ± 20	-13.6	21.3	3.39	cal AD 810–1270	cal AD 920–1180
UCIAMS-223311	Kugusugaruk	P381123-0	Metacarpal	1745 ± 20	-12.9	21.1	3.23	cal AD 760–1240	cal AD 880–1150
UCIAMS-223312	Kugusugaruk	P381120-0	Rib	1735 ± 15	-13.0	21.6	3.27	cal AD 770–1240	cal AD 890–1160
UCIAMS-223313	Kugusugaruk	P381106-0	Thoracic vertebra	1680 ± 15	-13.5	21.4	3.29	cal AD 830–1280	cal AD 950–1210
UCIAMS-223314	Kugusugaruk	P381096-0	Talus	1730 ± 15	-13.2	21.8	3.30	cal AD 770–1240	cal AD 890–1160
UCIAMS-223315	Kugusugaruk	P381100-0	Talus	1725 ± 15	-15.1	21.1	3.90	cal AD 650–1090	cal AD 720–980
UCIAMS-223316	Kugusugaruk	P381102-0	Metatarsal	1720 ± 15	-13.1	21.8	3.20	cal AD 790–1250	cal AD 900–1260
UCIAMS-223317	Kugusugaruk	P381115-0	Clavicle	1690 ± 15	-14.0	21.4	3.40	cal AD 810–1270	cal AD 920–1180
UCIAMS-223309	Nunavak	P381116-0	Cervical vertebra	1785 ± 15	-14.5	21.5	3.60	cal AD 660–1130	cal AD 760–1030
UCIAMS-210682	Nunavak	P381095-0	Clavicle	1695 ± 20	-13.1	20.7	3.30	cal AD 810–1280	cal AD 930–1190
UCIAMS-210683	Nunavak	P381111-0	Rib	1735 ± 15	-13.0	20.3	3.34	cal AD 770–1240	cal AD 890–1150
UCIAMS-223310	Kugok	P365899-0	Petrous	1840 ± 15	-12.4	20.2	3.21	cal AD 670–1130	cal AD 770–1030

TABLE 4. Summary statistics for the North Slope Birnirk Inuit population.

Statistic	Value	SD
Number of individuals (N)	22	
Number of haplotypes (K)	6	
Number of segregating sites (S)	9	
Sequence coverage (bp)	348	
Haplotype diversity (h)	0.7835	± 0.0534
Nucleotide diversity (π)	0.007514	± 0.004659
Mean pairwise difference (Π)	2.614719	± 1.453089

TABLE 5. Pairwise F<sub>st</sub> estimations based on HVR-1 sequence data of Birnirk individuals sampled by site from the Alaskan North Slope. The significant p-value (≤ 0.05) is bolded.

	Kugok	Kugusugaruk	Nunavak	Pigniq
Kugok				
Kugusugaruk	-0.19065			
Nunavak	0.81250	<b>0.61619</b>		
Pigniq	0.31081	0.21082	0.78453	

TABLE 6. Pairwise F<sub>st</sub> estimations based on HVR1 sequence data of Birnirk, Thule, and contemporary Inuit individuals sampled from the Alaskan North Slope. The significant p-value (≤ 0.05) is bolded.

	North Slope Birnirk Inuit	North Slope Thule Inuit
North Slope Inupiat		
North Slope Birnirk Inuit N = 22 (This study)		
North Slope Thule Inuit N = 39 (Tackney et al., 2019)	0.02926	
North Slope Inupiat N = 148 (Raff et al., 2015)	0.01342	<b>0.07487</b>

sites are exclusively representative of mitochondrial lineage A2a), while Canadian Thule, Alaskan Thule, and Canadian contemporary Inuit are separated based on a higher ratio of the A2b1 haplotype within these populations. Birnirk and contemporary Inupiat from the Alaskan North Slope are shown to cluster with the individuals at Uelen and Ekven, contemporary Yupik from the Chukotka Peninsula, Greenlandic Thule, and Greenlandic contemporary Inuit.

DISCUSSION

The Birnirk population on the North Slope of Alaska provides valuable insight regarding our understanding of Inuit population history over the last 1500 years. During the Birnirk period, maternal genetic continuity of the North Slope sites is evident. The 22 Birnirk individuals characterized in these analyses primarily exhibit haplotypes A2a and A2b1. Lineage D4b1a2a1a is carried at a lower frequency. Not all lineages were sampled at each locality (Fig. 2). Pairwise F<sub>st</sub> estimates suggest population subdivision (Table 5), however, low sample counts at three of the four sites and use of single locus data limit

TABLE 7. Mitochondrial HVR-1 sequence diversity estimates among known past and contemporary Inuit populations.

Inuit population	N	Sequence diversity	References
North Slope Birnirk	22	0.7835 ± 0.0534	This study
North Slope Iñupiat	148	0.7868 ± 0.0209	Raff et al., 2015
North Slope Thule	39	0.7584 ± 0.0612	Tackney et al., 2019
Greenlandic Thule	8	0.6786 ± 0.1220	Gilbert et al., 2007
Canadian contemporary Inuit	87	0.7033 ± 0.0443	Helgason et al., 2006
Greenlandic contemporary Inuit	517	0.7015 ± 0.0151	Helgason et al., 2006; Gilbert et al., 2008; Lopopolo et al., 2016; Saillard et al., 2000
Siberian contemporary Yupik (Sireniki, Chaplin, Naukan)	128	0.7360 ± 0.0330	Derbeneva et al., 2002; Volodko et al., 2008

TABLE 8. Mitochondrial haplotype frequency estimates of known past and contemporary Inuit used in the principal component analysis (Fig. 3) to visualize maternal relatedness across populations.

Inuit population	N	A2	A2a	A2b1	D4b1a2a1a	D2a	Non-Inuit	References
Uelen/Ekven Past	33	0.000	0.515	0.242	0.242	0.000	0.000	Flegontov et al., 2019; Sikora et al., 2019
Paipelghak Birnirk	5	0.000	1.000	0.000	0.000	0.000	0.000	Raghavan et al., 2014
Siberian contemporary Yupik (Sireniki, Chaplin, Naukan)	133	0.008	0.534	0.263	0.075	0.173	0.000	Derbeneva et al., 2002; Volodko et al., 2008
North Slope Birnirk	22	0.000	0.455	0.364	0.182	0.000	0.000	This study
North Slope Thule	39	0.000	0.256	0.667	0.077	0.000	0.000	Tackney et al., 2019
North Slope Iñupiat	148	0.007	0.554	0.351	0.047	0.027	0.014	Raff et al., 2015
Precontact Nunalleq	28	0.000	1.000	0.000	0.000	0.000	0.000	Raghavan et al., 2014
Canadian Thule	15	0.000	0.000	0.800	0.200	0.000	0.000	Raghavan et al., 2014
Canadian contemporary Inuit	88	0.114	0.148	0.614	0.125	0.000	0.000	Helgason et al., 2006
Greenlandic Thule	25	0.000	0.640	0.360	0.000	0.000	0.000	Gilbert et al., 2007; Raghavan et al., 2014
Greenlandic contemporary Inuit	518	0.006	0.431	0.531	0.031	0.000	0.000	Helgason et al., 2006; Gilbert et al., 2008; Lopopolo et al., 2016; Saillard et al., 2000

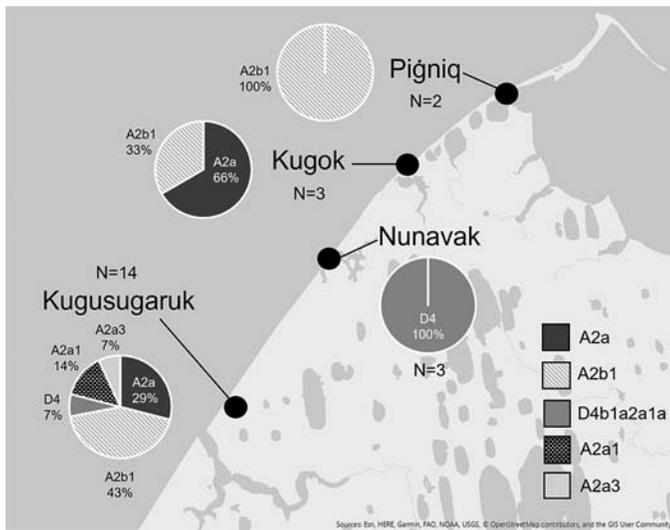


FIG. 2. Division of haplotype frequencies among Birnirk sites on the North Slope.

this analysis. Similarity in dating (Table 3) and close geographical proximity among localities (Fig. 1) suggest the individuals buried at all four sites likely represent one population occupying the area over a 200–300-year period.

The material cultural relationship of Birnirk as part of the Inuit tradition has been recognized since it was described, but their genetic affiliation remained unclear because of limited sampling. The identification of lineages A2a, A2b1, and D4b1a2a1a, as well as A2a1 and A2a3 on the North Slope (Table 2) confirm this Birnirk population is maternally related to Thule and contemporary Inuit. Birnirk

### Inuit Principal Component Analysis

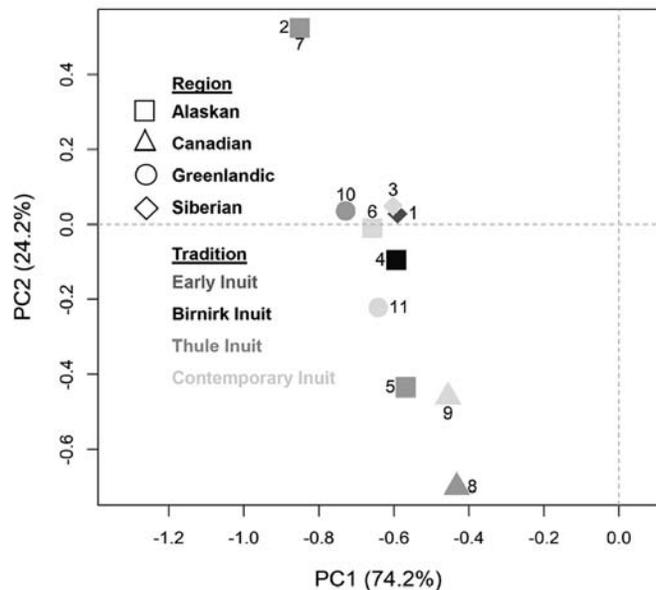


FIG. 3. Principal component analysis constructed from Inuit mtDNA haplotype frequency data (Table 8). (1) Uelen/Ekven Past Inuit, (2) Paipelghak Birnirk Inuit, (3) Siberian contemporary Yupik (Sireniki, Chaplin, Naukan), (4) North Slope Birnirk Inuit, (5) North Slope Thule Inuit, (6) North Slope Iñupiat, (7) Precontact Nunalleq, (8) Canadian Thule Inuit, (9) Canadian contemporary Inuit, (10) Greenlandic Thule Inuit, and (11) Greenlandic contemporary Inuit.

and Thule Inuit also share a private mutation, m.16212A>G within the A2b1 lineage at the Pigniq site and Nuvuk cemetery (Tackney et al., 2019). This private mutation is

also present at a low frequency in contemporary Inuit of Canada, Greenland, and the Chukotka Peninsula, further suggesting a large shared gene pool (Helgason et al., 2006; Gilbert et al., 2008; Lopopolo et al., 2016). Pairwise  $F_{st}$  estimates (Table 6) between the Birnirk population sampled here, the Thule Inuit at Nuvuk (Tackney et al., 2019), and the Iñupiat of the North Slope (Raff et al., 2015) indicate that the archaeologically defined Birnirk and Thule cultures are not maternally genetically distinct populations. Rather, Birnirk and Thule Inuit represent a continuation of maternal genetic motifs through the archaeological transition. Based on the mitogenome data presented here (Table 7), the maternal genetic diversity seen within the North Slope region was maintained throughout the eastward Thule migration and transition into contemporary Inuit culture.

Birnirk sites and isolated finds are spread across vast coastal distances from the Kolyma River to the western Canadian Arctic (Mason, 2016a). Therefore, Birnirk Inuit likely had a major role expanding the Inuit gene pool across the Bering Strait. To investigate, we compiled available haplotype frequency data from all published Inuit populations (Table 8). Clustering of the North Slope Birnirk Inuit and past Inuit from Uelen and Ekven (Fig. 3) offers support for bidirectional maternal gene flow between these maritime focused people. Birnirk individuals buried on the North Slope (cal. AD 650–1300) and individuals at Uelen and Ekven (cal. 125 BC–AD 1485) (Flegontov et al., 2019; Sikora et al., 2019) were either members of the same population that frequently traveled the Chukchi Sea or shared a common parent population or both. Evidence presented here suggests Birnirk was a genetic intermediary population linking past Inuit of the Chukotka Peninsula to the Thule Inuit in the North American Arctic. Clearer cultural affiliations for individuals from Uelen and Ekven are needed to further test this hypothesis.

It is unknown whether Birnirk Inuit are partially or entirely descendant from populations from the Chukotka Peninsula, and determination awaits future genome-wide analyses. However, BEAST maximum likelihood estimated coalescence times from Dryomov et al. (2015) for the mitochondrial haplotypes sampled here (~3.94 kya for A2a, 2.07 kya for A2b1, and 4.34 kya for D4b1a2a1a) predate the Birnirk culture and their proposed ancestors, Old Bering Sea. These coalescence dates suggest these lineages should be found in even more ancestral populations, perhaps before the appearance of the Inuit cultural tradition entirely or

external to the surrounding Bering Strait region. Continued research of past Inuit population histories based on well-dated, clearly affiliated human remains across the Bering Strait region may further clarify the genetic origins and contributing populations of the Birnirk Inuit and the early period of the Inuit tradition.

## CONCLUSION

This research builds upon our previous understanding of the peopling of the Arctic, specifically the ancestral maternal lineages of the Inuit tradition. The mitochondrial data presented here represent individuals from the most clearly associated Birnirk archaeological context known. These data also constitute the first Birnirk sequence data east of the Bering Strait. The detection of lineages A2a, A2b1, and D4b1a2a1a confirm this Birnirk population as an ancestral component of the Thule Inuit. We demonstrate that Birnirk share much of their maternal gene pool with past Inuit groups from Siberia, likely facilitated by bidirectional gene flow. Further genome-wide and archaeological data from Birnirk individuals in the Utqiagvik area will provide an increased understanding of the genetic diversity between the archaeologically distinct Birnirk and Thule Inuit populations in the North Slope region.

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