



Ancient DNA evidence for genetic continuity in arctic dogs

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ABSTRACT

The domestic dog fulfills many functions for their human companions, such as hauling, guarding, and protection. Consequently, humans have taken dogs to nearly every corner of the globe. Recent translocations of Western dogs stemming from the Victorian era dog fancy have erased some of the ancient genetic signatures of these earlier migrations. Here we used DNA of ancient and modern dogs from the North American Arctic of Alaska and Greenland to assess their genetic continuity in time and space. We successfully sequenced 23 archaeological (ca. AD 1250–1910) and recent (ca. AD 1930–1990) surface-collected *Canis* bone and tooth samples and compared them to 51 modern Inuit Sled Dogs and to published sequences of modern Alaskan Malamutes (and additional Inuit Sled Dogs) to test for evidence of lineage replacement or genetic continuity through time. Ancient samples from Alaska and Greenland and modern sequences from Greenland all contained a high frequency of haplotype A31, which was previously described only in modern North American Arctic dogs. Thus, A31 was a common thread tying the entire North American Arctic together prior to European colonization and, in the Eastern Arctic, indicates genetic continuity between past and present dogs as well. However, A31 is rare in modern Alaskan dogs, consistent with post-colonization replacement by Eurasian matrilineal.

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1. Introduction

Since the domestication of the dog approximately 15,000 years ago, humans and their canine companions have been inextricably linked (Morey, 2006, 2010; Savolainen et al., 2002; Vilà et al., 1997). The early peoples that colonized North America initially ca. 14,000 years ago (e.g., Kitchen et al., 2008; Reich et al., 2012; Schurr, 2004; Torroni et al., 1992) apparently brought domestic dogs with them on their migrations (Barta, 2007; Leonard et al., 2002; Tito et al., 2011). Late Pleistocene examples have yet to be reported, and early Holocene examples in the Americas are rare (e.g., Grayson, 1988; Haag, 1970; McMillan, 1970; Morey and Wiant, 1992; Tuck, 1976; Walker et al., 2005).

Domestic dogs probably fulfilled roles as haulers, guarders, and, at times, food animals. North America experienced at least one subsequent wave of canine colonization, that from Europe beginning in the late 15th century and continuing into the present (e.g., Schwartz, 1998; Snyder and Leonard, 2006, 2011). This wave of European domestic dogs has to a large extent supplanted Native

American dogs and their genetic signature(s) (Castroviejo-Fisher et al., 2011; Leonard et al., 2002). However, novel mitochondrial DNA haplotypes, similar to ones otherwise found only in East Asia, still occur in dogs of the North American Arctic, suggesting that parts of this region may have escaped European replacement (Klüttsch et al., 2010; Pang et al., 2009). Although it seems likely that much of the indigenous dog gene pool of the western North American Arctic has been replaced over the past century, subsequent to the gold rush and beginning of sled-dog racing as a sport in the 1930s (Coppinger and Coppinger, 2001; Huson et al., 2010). Canadian Eskimo dogs and Greenland dogs (hereafter “Inuit Sled Dogs”) of the Eastern Arctic potentially maintained their indigenous ancestry. Here, we use ancient and modern DNA of Arctic dogs to directly test whether modern-day Eastern Arctic dog haplotypes reflect genetic continuity with their pre-Columbian forebears, and whether pre-Columbian dogs of the Western Arctic composed the same genetic stock.

Nowhere is the use of dogs more linked to humans than in the Arctic. To Canadian Inuit, the sled dog is the animal most symbolic of their region. Early 18th century missionaries described sled-dog teams of up to 28 dogs in Labrador (Taylor, 1974). On May 1, 2000, Nunavut adopted the *qimmiq* or Inuit Sled Dog (formerly called the Canadian Eskimo Dog) as the official animal emblem for the new Canadian territory. Preservation of this indigenous dog breed is

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intimately linked to Inuit identity, and its precipitous decline less than 50 years ago marks a political flashpoint tied to relocation and settlement (Montcombroux, 2002). Some sources estimate that 20,000 dogs died during this period, particularly on Baffin Island and in Nunavik (Northern Québec), but the genetic effect is unknown.

The importance of dogsleds to prehistoric people was first described by Therkel Mathiassen (1927) who, based on his excavations at Naujan in the central Canadian Arctic, used dogsleds as part of a suite of characteristics to define “Thule” culture, which dates from ca. AD 1000 to contact. Since this time dogs have been recovered from nearly every Thule culture archaeological site from Siberia to Greenland and many of these, particularly in the Eastern Arctic (Canada and Greenland), have artifacts associated with dogsled traction (e.g., Maxwell, 1985; Morey, 2010).

The earlier archaeological cultures, generally subsumed under the moniker Arctic Small Tool tradition (ASTt), derive from eastern Siberia, possibly from middle Neolithic Bel’kachinsk (Hoffecker, 2004) cultures. These were the first people to populate the Canadian Arctic archipelago and Greenland. Dogs have been clearly identified from well-dated contexts in the earliest ASTt sites (ca. 2500 BC) in West Greenland (Gotfredsen, 1998; Meldgaard, 2004; Møhl, 1986). Recent ancient DNA (aDNA) analysis of human hair from one of these sites (Gilbert et al., 2008; Rasmussen et al., 2010), connects this initial population to Siberia and the Bering Strait region, but with a genetic signature different from Thule or recent Arctic people (e.g., Crawford, 2007; Hayes et al., 2003, 2005; Helgason et al., 2006).

Putative dog remains have been identified from at least 10 early ASTt or Paleoeskimo sites in Canada (Morey, 2010; Morey and Aaris-Sorensen, 2002). The oldest potential dog remains in northern Alaska are from the Old Whaling site at Cape Krusenstern, ca. 1300–800 BC (Darwent, 2006; Giddings and Anderson, 1986), although the artifacts and architecture are clearly not associated with ASTt. Other early ASTt sites in northern Alaska with identified dog remains include Choris, Battle Rock and Kugzruk in the Kotzebue Sound – Seward Peninsula region (Giddings and Anderson, 1986). In the Eastern Arctic, at least 12 later ASTt sites, referred to as Dorset (ca. 800 BC–AD 1200), have dog or putative dog remains that may reflect sporadic connections with Alaska or, more likely, represent an *in situ* development of this small dog population possibly supplemented by breeding with local wolves or Native dogs from the south (Cleland and Haag, 1973; Friesen, 2000; Maxwell, 1985; McGhee, 1996; Nagy, 2000; Prentiss and Lenert, 2009). Late Dorset (ca. AD 500–1200) dogs also have the potential to reflect a Norse influence (Sutherland, 2000).

In Alaska, several archaeological cultures postdating ASTt developed in the Bering Strait region which are defined on the basis of distinctive artistic styles (Mason, 1998) and include Ipiutak and Old Bering Sea (OBS). Dog remains have been identified from several Ipiutak and OBS deposits in Alaska (Collins, 1937; Geist and Rainey, 1936; Giddings and Anderson, 1986; Larsen and Møhl, 2001; Larsen and Rainey, 1948). Most likely the Siberian late Neolithic Ymyakhtakh culture gave rise to cultures in the Bering Strait region including OBS, which developed into Birnirk–Thule around AD 1200–1000 (Hoffecker, 2004; Mason, 1998, 2009). Jenness (1940) suggested that around “the end of the Birnirk phase at Barrow... a larger, sturdier breed of dog was introduced in Arctic America from Siberia where dog traction [arose, and]... certain bands of these north Alaskan Eskimo trekked eastward, carrying their Thule culture with them.” McGhee (1969/70, 1975) proposed a movement of Thule into the Canadian Arctic following a High Arctic route and then spreading south and west. Morrison (1983) and Arnold and Stimmel (1983) both postulated a secondary expansion of Thule from the west along the mainland coast based

on the close connection between the artifacts in the western Canadian Arctic and Alaska and not to Canada/Greenland. This scenario seems to be supported by older radiocarbon dates and artifacts of Alaskan Thule-style in the High Arctic (McCullough, 1989; Schlederemann and McCullough, 1980) and younger dates in the western Canadian Arctic (Friesen, 2004; Friesen and Arnold, 2008). Open water hunting and dogsled traction would have given these highly mobile groups a strong advantage over the Dorset (Friesen, 2000).

Recent genetic efforts have provided a snapshot of modern domestic dog mitochondrial genetic diversity and its pattern of geographic distribution (Pang et al., 2009; Savolainen et al., 2002). These studies have elucidated the haplotypes that are most common throughout the world (UT: Universal Type) and those that show a more restricted geographic distribution (Pang et al., 2009; Savolainen et al., 2002). Modern Arctic dogs possess both common (e.g., A18, A20) and geographically restricted haplotypes such as A31, which has only been reported from the North American Arctic. Examining the frequency of such widespread and geographically restricted haplotypes through time allows us to directly confirm or refute their putative indigenous heritage and to estimate the degree to which modern Arctic dogs have been influenced by Westernized breeds.

Here, we investigate mtDNA of dog remains associated with the archaeological Thule culture and their putative descendants the Inuit Sled Dog. Recent excavations at Cape Espenberg in western Alaska and Inglefield Land, Northwest Greenland have yielded numerous dog remains from well-dated contexts that can be used to characterize the prehistoric genetic profile of indigenous breeds. We utilized ancient and modern Arctic dogs to 1) determine if purportedly indigenous Eastern Arctic haplotypes (e.g., A31; Klütsch et al., 2010; Pang et al., 2009) occur in ancient samples of the eastern and western North American Arctic and 2) if modern Eastern Arctic dog breeds have been influenced by Westernized breeds.

2. Materials and methods

Cape Espenberg is located on the farthest southwestern extent of Kotzebue Sound, Alaska, just above the Arctic Circle (Fig. 1). It consists of a series of dune-covered beach ridges that jut out into the sound and have been building over the past 4000 years. Between 2009 and 2011, the Cape Espenberg Project (CEP)—a multi-disciplinary research project focused on exploring Thule culture (ancestors of the modern Iñupiaq people) origins in Northwest Alaska—undertook excavation of six Thule house depressions (Hoffecker and Mason, 2010, 2011). For this study we sampled *Canis* remains recovered during the 2009 (KTZ-087, Feature 87) and 2010 field seasons (KTZ-087, Feature 68a; KTZ-088, Feature 33; KTZ-304, Feature 21). Feature 21 is the oldest house in this sample and was occupied around AD 1260–1400, followed by F. 87 (ca. AD 1275–1450), F. 68a (ca. AD 1450–1650), and F. 33 (ca. AD 1675–1800). Thus these houses provided samples from across the Thule occupation of the beach ridges (Table 1; see Table 2 for associated radiocarbon dates). To prevent sampling the same individual more than once we selected the maximum number of a given skeletal element within each archaeological feature (also known as the Minimum Number of Individuals; see Lyman, 2008). A total of 12 pre-contact samples from four archaeological features were selected for aDNA amplification, which span nearly the entire Thule sequence at Cape Espenberg.

Inglefield Land is located in Northwest Greenland adjacent to Smith Sound (Fig. 1); it is considered to be the main entry point for prehistoric indigenous populations of Greenland who originated in Alaska and made their way across the Canadian Arctic. The

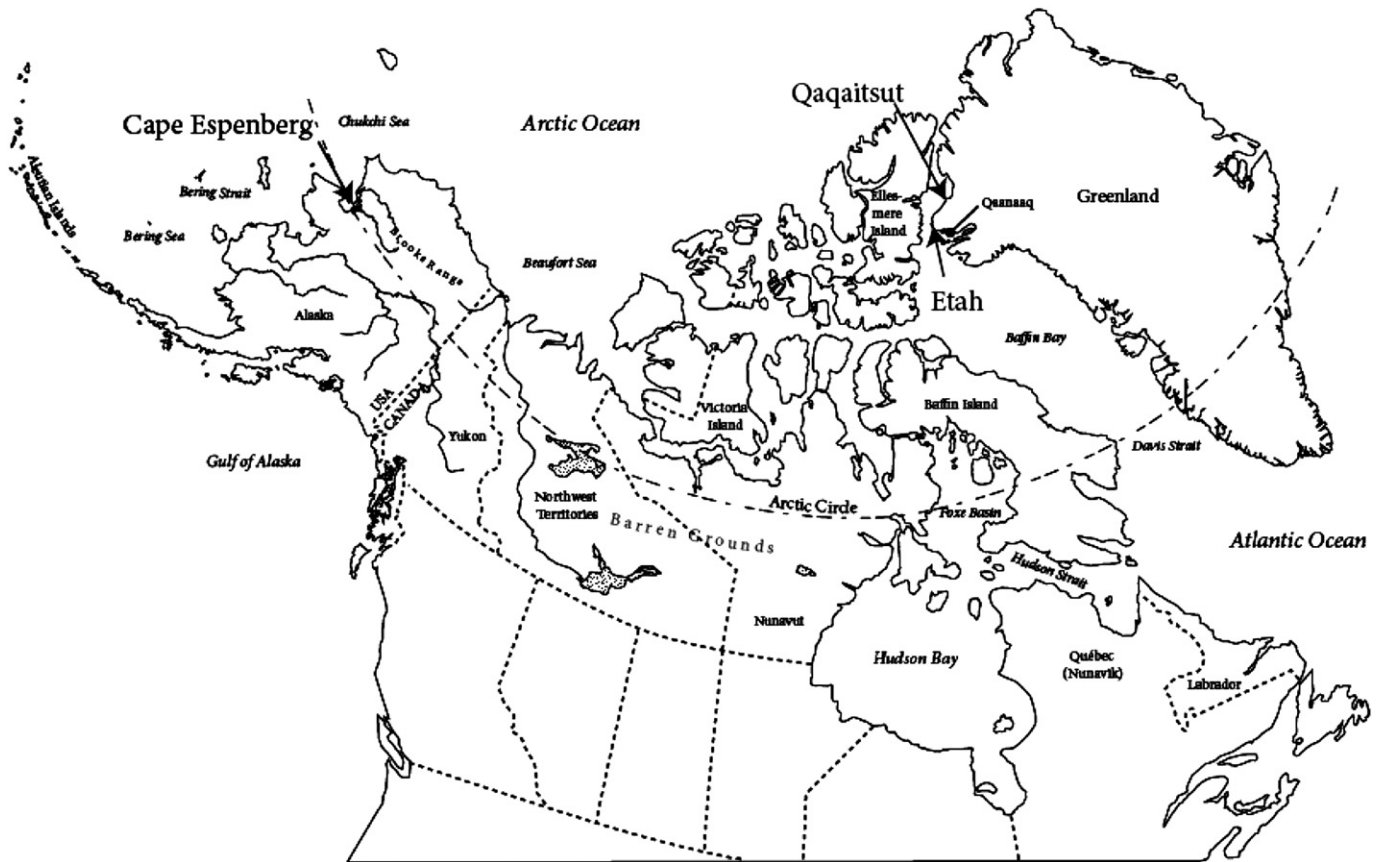


Fig. 1. Map of the North American Arctic, and our sampling sites (indicated by arrows). Cape Espenberg in Alaska, and Qaqaitsut and Etah in North West Greenland.

Inglefield Land Archaeology Project (ILAP) was a multi-year research project focusing on the more recent prehistory of Inglefield Land. The project began in 2004 with large-scale foot (occasionally supplemented by a small boat), and helicopter survey recording cultural features from ca. 4000 years of prehistoric and historic occupation (Darwent et al., 2007; Darwent et al., 2008). Fieldwork continued through 2009 with excavations at four sites over three field seasons in western, central and eastern Inglefield Land (LeMoine and Darwent, 2010).

Two Inughuit houses were excavated at the site of Etah (Fig. 1) in western Inglefield Land in 2006. Based on the age of the recovered historical artifacts Feature 1 was inhabited after AD 1900 but before occupation of the site by Donald MacMillan's Crockerland expedition in 1913–1917 (LeMoine and Darwent, 2010). The second house, F. 2, was occupied in the mid-late 1800s based on age of associated artifacts and coincides with both the time of Elisha Kent Kane and Robert Peary's expeditions to the region. A buried early-Thule deposit (ca. AD 1275–1650), which included a sleeping platform and floor area, was encountered under F. 1 (Table 2). These excavations yielded over 25,000 bones primarily identified as the remains of small dovekies but also included numerous *Canis* specimens (Johansen, 2012) from which five non-overlapping mandible samples were obtained.

In 2009 excavation at the site of Qaqaitsut (Fig. 1) in Paris Fjord, eastern Inglefield Land produced an unusual concentration of dog remains from one early Thule (ca. AD 1275–1440) dwelling and its associated stone meat cache (Table 2). Of the 264 specimens that could be identified to the level of family or lower taxonomic level, 20% of these were identified as *Canis*. The house itself (F. 2) was quite unremarkable, and yielded a relative dearth of formed

artifacts, but this house hinted at a harsh winter and a sled-dog team that served as sustenance rather than transport. Nearly all of the dog remains were concentrated in the kitchen area of the house and exhibited extensive cut marks and cracking of the bones to release the marrow. A fragment of a mandible from a stone cache (F. 7) was refit to the other portion from recovered from the house feature more than 15 m away, thereby linking their occupation. From these two features at Qaqaitsut seven dog mandibles were sampled.

In addition to 21 pre-contact archaeological samples and four post-contact archaeological samples, three modern samples were opportunistically collected from the surface of sites in Inglefield Land known to have been occupied between 1930 and 1990 (Innuarfissuaq, $n = 2$; Qaqaitsut, $n = 1$), for a total of 28 field-collected samples (Table 1). The early Thule period site of Innuarfissuaq was excavated by Erik Holtved in the 1930s (Holtved, 1944) and his crew included Inughuit families and their dogs. This location continued to be visited by hunters from the modern villages of Qaanaaq and Siorapaluk until the 1990s. We also collected a dog cranium from the surface of Qaqaitsut, which had been used by at least five families who established a short-term settlement there ca. 1985–1990.

Dogs in coastal Arctic sites would have consumed marine mammals regularly, and thus none were dated directly because of issues associated with the marine reservoir effect, which can yield results 300–800 years older than terrestrial animal samples from the same context (e.g., Stuiver and Braziunas, 1993). All radiocarbon dates come from associated caribou, arctic hare, or short-lived plant species and were corrected for isotopic fractionation (Morlan, 1999) and calibrated to two-sigma following Reimer et al.

Table 1
Canis skeletal specimens collected in western Alaska ($n = 13$) and in Northwest Greenland ($n = 15$) listed in chronological order based on associated radiocarbon dates (see Table 2), context, and/or temporally diagnostic artifacts. BELA is the National Park Service's accession code for Bering Land Bridge National Park and Preserve, KNK is the accession code for the Greenland National Museum and Archives (*Kalaallisut Nunatta Katersugaasivia*), and UCDZL is the Zooarchaeology Laboratory at the University of California, Davis.

Specimen number	Site/locality	Feature	Provenience	Skeletal element	Portion	Taphonomy	Age	Time period	Context
BELA-00112-36034	KTZ-304, Cape Espenberg, Alaska	F. 21, House	Unit 4N, 3E; Level 1e (side spur kitchen area)	Cranium	Complete	Impact scar + two holes in frontals (fresh fractures)	Adult; no tooth wear	Early Thule (ca. AD 1260–1400)	Pre-contact
BELA-00112-36035	KTZ-304, Cape Espenberg, Alaska	F. 21, House	Unit 4N, 6E; Level 1e (tunnel)	Cranium	Maxilla + orbits	n/a	Adult; no tooth wear	Early Thule (ca. AD 1260–1400)	Pre-contact
BELA-00112-37373	KTZ-304, Cape Espenberg, Alaska	F. 21, House	9N, 4E; Level 2a (house interior)	Mandible	Body, right	Moderate weathering	Adult; no tooth wear	Early Thule (ca. AD 1260–1400)	Pre-contact
BELA-00112-37374	KTZ-304, Cape Espenberg, Alaska	F. 21, House	9N, 3E; Level 2a (house interior)	Mandible	Complete, right	n/a	Adult; slight tooth wear	Early Thule (ca. AD 1260–1400)	Pre-contact
BELA-00112-37375	KTZ-304, Cape Espenberg, Alaska	F. 21, House	Unit 4N, 2E; Level 2a (side spur kitchen area)	Mandible	Complete, right	n/a	Adult; slight tooth wear	Early Thule (ca. AD 1260–1400)	Pre-contact
BELA-00112-37376	KTZ-304, Cape Espenberg, Alaska	F. 21, House	5N, 4E; Level 1c (tunnel/kitchen spur)	Mandible	Mandibular condyle to mesial end, right	Chopped parallel to body under M2 on labial surface	Adult; no tooth wear, alveolar absorption of P4 adult	Early Thule (ca. AD 1260–1400)	Pre-contact
BELA-00109-35135	KTZ-087, Cape Espenberg, Alaska	F. 87, House	Unit 5S, 6E; Level 2	Calcaneus	complete, right	moderate weathering	Adult; slight tooth wear	Early Thule (ca. AD 1275–1450)	Pre-Contact
BELA-00115-37940	KTZ-087, Cape Espenberg, Alaska	F. 87, House	Unit 9S, 3E Level 2E (kitchen "ritual feature")	Maxillary canine	Complete, left	Grooved around circumference of root; "pendant" (TL = 51 mm)	Adult; slight tooth wear	Early Thule (ca. AD 1275–1450)	Pre-contact
BELA-00112-37370	KTZ-087, Cape Espenberg, Alaska	F. 68a, House	Unit 9N, 3E; Level 3b (house/cold-trap entrance)	cranium	maxillary fragment, left	n/a	adult; no tooth wear	Middle Thule (ca. AD 1450–1650)	Pre-Contact
BELA-00112-37371	KTZ-087, Cape Espenberg, Alaska	F. 68a, House	Unit 7N, 4N; Level 3a (tunnel)	Mandible	Complete, left	n/a	Adult; heavy tooth wear	Middle Thule (ca. AD 1450–1650)	Pre-contact
BELA-00112-37367	KTZ-088, Cape Espenberg, Alaska	F. 33, House	Unit 10N, 1E; Level 1b (tunnel)	radius + ulna	Prox + 1/2 shaft, right	Spiral fracture at midshaft; carnivore gnawing on prox end	Adult; fused	Late Thule-Inūpiat (ca. AD 1675–1800)	Pre-contact
BELA-00112-37368	KTZ-088, Cape Espenberg, Alaska	F. 33, House	Unit 6N, 6E; Level 1b (side spur kitchen area)	Radius + ulna	Prox + 3/4 shaft, right	Carnivore gnawing on both ends	Adult; fused	Late Thule-Inūpiat (ca. AD 1675–1800)	Pre-contact
BELA-00112-37369	KTZ-088, Cape Espenberg, Alaska	F. 33, House	Unit 4N, 2E; Level 2b (front of sleeping platform)	Radius + ulna	Complete, right	4 fine cuts on distal posterior shaft of ulna	Adult; fused (osteophytic lipping at distal articulation)	Late Thule-Inūpiat (ca. AD 1675–1800)	Pre-contact
KNK492-36	Qaqaitsut West, Paris Fjord, Greenland	F. 2, House	Unit 2N, 3E; Level 1 (kitchen area)	Mandible	Complete, left (horizontal ramus, right)	Fine cut marks, lateral/inferior surface; mesial canine scorched	Adult; no tooth wear	Early Thule (ca. AD 1275–1440)	Pre-contact
KNK492-37	Qaqaitsut West, Paris Fjord, NW Greenland	F. 2, House	Unit 2N, 3E; Level 1 (kitchen area)	Mandible	Horizontal ramus, left (complete, right)	Fine cut marks, lateral/inferior surface	Adult; slight tooth wear	Early Thule (ca. AD 1275–1440)	Pre-contact
KNK492-38	Qaqaitsut West, Paris Fjord, NW Greenland	F. 2, House	Unit 2N, 3E; Level 1 (kitchen area)	Mandible	Horizontal ramus, left	Ascending ramus carnivore gnawed off	Adult; no tooth wear	Early Thule (ca. AD 1275–1440)	Pre-contact
KNK492-39	Qaqaitsut West, Paris Fjord, NW Greenland	F. 2, House	Unit 3N, 3E; Level 1 (kitchen area)	Mandible	Complete, right; does not match left mandibles	Carnivore gnawing; weathered	Adult; slight tooth wear	Early Thule (ca. AD 1275–1440)	Pre-contact
KNK494-1	Qaqaitsut West, Paris Fjord, NW Greenland	F. 7, Cache	Unit 1N, 2E; Level 1	Mandible	Mesial 3/4 horizontal ramus, left	Cracked for marrow at gonial angle	Adult; no tooth wear	Early Thule (ca. AD 1275–1440)	Pre-contact
KNK494-2	Qaqaitsut West, Paris Fjord, NW Greenland	F. 7, Cache	Unit 1N, 2E; Level 1	Mandible	Mesial 3/4 horizontal ramus, left (horizontal ramus right)	Ascending ramus chopped off	Adult; no tooth wear	Early Thule (ca. AD 1275–1440)	Pre-contact
KNK494-3	Qaqaitsut West, Paris Fjord, NW Greenland	F. 7, Cache	Unit 1N, 2E; Level 1	Mandible	Mesial 3/4 horizontal ramus, left	Cracked for marrow at gonial angle (refits to ascending ramus from F. 2)	Adult; slight tooth wear	Early Thule (ca. AD 1275–1440)	Pre-contact

KNK2643-1838	Etah, Foulke Fjord, NW Greenland	F. 1, House	Unit 1S, 6E; Level 5 (buried house floor)	Mandible	Complete, right	n/a	Juvenile; deciduous premolars (2 –6 mos)	Early Thule (ca. AD 1275–1650)	Pre-contact
KNK2644-1119	Etah, Foulke Fjord, NW Greenland	F. 2, House	Unit 2N, 3E; Level 3 house interior)	Mandible	Horizontal ramus, left	Charred (mottled black)	Juvenile; deciduous premolars (2 –6 mos)	Historic Inughuit (ca. AD 1850–1900)	Post-contact
KNK2644-1120	Etah, Foulke Fjord, NW Greenland	F. 2, House	Unit 1N, 2E; Level 6 (house interior)	Mandible	Complete, left	Alveolar resorption with infection, missing P4-M1	Old adult; heavy tooth wear	Historic Inughuit (ca. AD 1850–1900)	Post-contact
KNK2644-1121	Etah, Foulke Fjord, NW Greenland	F. 2, House	Unit 4N, 3E; Level 3 (house interior)	Mandible	Complete, right	n/a	Adult; slight tooth wear	Historic Inughuit (ca. AD, 1850–1900)	Post-contact
KNK2643-1839	Etah, Foulke Fjord, NW Greenland	F. 1, House	Unit 9N, 4E; Level 4 (house interior)	Mandible	Complete, right	n/a	Juvenile; deciduous premolars (2 –6 mos)	Historic Inughuit (ca. AD 1900–1910)	Post-contact
UCDZL-1081	Innuarfissuaq Marshall Bay, NW Greenland	Surface	n/a	Cranium	Complete	Alveolar resorption with infection, missing P4-M1	Old adult; moderate tooth wear	Modern sled dog (ca. AD, 1930–1990)	Post-contact
UCDZL-1082	Innuarfissuaq Marshall Bay, NW Greenland	Surface	n/a	Cranium	Complete	Healed wound to left frontal; spiral fracture hole in right parietal; alveolar resorption of P2	Old adult; heavy tooth wear	Modern sled dog (ca. AD 1930–1990)	Post-contact
UCDZL-1080	Qaqaitsut, Paris Fjord, NW Greenland	Surface	n/a	Cranium	Complete, no teeth	Healed wound to left frontal; bullet hole through right parietal	Adult; moderate tooth wear	Modern sled dog (ca. AD 1980–1990)	Post-contact

Table 2Radiocarbon dates associated with *Canis* skeletal remains sampled from Thule period sites in western Alaska and Northwest Greenland.

Lab number	Site/feature	Provenience	Material	Conventional ¹⁴ C age BP	Delta ¹³ C value	2-Sigma calibrated age (Intcal09.14) ^a	Reference
AA88105	Qaqaitsut West, Feature 2	Unit 1N, 5E; NE Quad; Level 2 (house, tunnel)	Caribou premolar	547 ± 42	–18.8	AD 1304–1440	This publication
AA88106	Qaqaitsut West, Feature 2	Unit 2N, 3E; SW Quad; Level 2 (house, kitchen area)	Caribou femur	649 ± 43	–17.6	AD 1278–1398	This publication
Beta233266	Etah, Feature 1	Unit 1S, 6E; NW Quad; Level 5 (buried house, floor)	Caribou astragalus	260 ± 40	–19.5	AD 1492–1950 ^b	LeMoine and Darwent, 2010
Beta233261	Etah, Feature 1	Unit 0N, 5E; NE Quad; Level 6 (buried house, sleeping platform)	Arctic bell heather	330 ± 40	–28.3	AD 1465–1645	LeMoine and Darwent, 2010
Beta233262	Etah, Feature 1	Unit 1N, 5E; NW Quad; Level 7 (buried house, sleeping platform)	Arctic hare tibia	450 ± 40	–22.9	AD 1405–1617	LeMoine and Darwent, 2010
Beta233263	Etah, Feature 1	Unit 1N, 4E; NW Quad; Level 9 (buried house, sleeping platform)	Arctic hare radius	360 ± 40	–22.9	AD 1449–1635	LeMoine and Darwent, 2010
Beta233264	Etah, Feature 1	0N, 5E; NW Quad; Level 8 (buried house, sleeping platform)	Arctic hare pelvis	660 ± 40	–21.9	AD 1273–1396	LeMoine and Darwent, 2010
Beta285168	KTZ-304, Feature 21	Unit 6N, 4E; SE Quad; Level 1e (house, tunnel)	Caribou femur, distal epiphysis	680 ± 40	–17.8	AD 1263–1394	Hoffecker and Mason, 2010, 2011
Beta286169	KTZ-304, Feature 21	Unit 6N, 4E; SE Quad; Level 1e (house, tunnel)	Caribou trapezoid-magnum	640 ± 40	–18.1	AD 1282–1398	Hoffecker and Mason, 2010, 2011
Beta286170	KTZ-088, Feature 33	Unit 5N, 1E; NW Quad; Level 2c (house, tunnel)	Caribou rib midshaft fragment	120 ± 40	–19.1	AD 1676–1941 ^b	Hoffecker and Mason, 2010, 2011
Beta286171	KTZ-087, Feature 68a	Unit 10N, 2E; SW Quad; Level 4b (house, under sleeping platform)	Caribou distal phalanx	250 ± 40	–18.5	AD 1514–1805 ^b	Hoffecker and Mason, 2010, 2011
Beta286172	KTZ-087, Feature 68a	Unit 10N, 3E; NW Quad; Level 4b (house, under sleeping platform)	Caribou middle phalanx	360 ± 40	–18.8	AD 1450–1635	Hoffecker and Mason, 2010, 2011

^a Reimer et al., 2009.^b Calibrated date overlaps with modern era; however, no contact-period artifacts were recovered from these deposits, thus they predate British/American contact in Smith Sound and Russian contact in Kotzebue Sound (ca. AD 1800).

(2009). Osteological measurements along with age, sex, and shoulder height estimates were made on all relevant samples prior to destructive analysis (Appendix A, B, C).

Additionally, 51 modern breed samples of Greenland ($n = 18$) and Canadian Inuit dogs ($n = 33$), obtained through the Center for Veterinary Genetics (Veterinary Genetics Laboratory, UC Davis), were utilized in the analysis as modern comparative material. Recent work utilizing 10 autosomal microsatellites suggests that there is little genetic differentiation between “Greenland dogs” and “Canadian Inuit dogs” (Andersen, 2005). In particular, the measured difference in allele frequencies between “Greenland dogs” and “Canadian Inuit dogs” in that study ($F_{ST} = 0.035$) was far lower than the average F_{ST} values distinguishing other recognized dog breeds (e.g., $F_{ST} = 0.33$; Parker et al., 2004). Therefore, we refer to both of these Arctic breeds collectively as Inuit Sled Dogs.

2.1. DNA extraction

DNA extractions were carried out in the Veterinary Genetics Laboratory (VGL) ancient DNA facility at the University of California, Davis. This facility is an isolated and dedicated animal ancient DNA laboratory equipped with an independent HEPA-filtered air source. No modern DNA work has ever been conducted in this facility. Laboratory surfaces and equipment are routinely sterilized with bleach and exposed to UV light. Additional controls include 1) sterile personal protective equipment (isolation gowns, shoe covers, face masks and hair covers), 2) extraction and PCR negative controls, and 3) separate buildings for pre- and post-PCR work.

Extractions were conducted in sets of nine samples and one negative control blank. Bone powder was obtained either by hand drilling into cortical bone or grinding a portion of bone/tooth with a mortar and pestle. Tooth/bone powder (100–250 mg) was transferred into a 15 ml sterile conical tube. Subsequently, procedures were identical for bone, tooth, and negative control samples. Extraction was carried out via the silica extraction method (Rohland and Hofreiter, 2007; Rohland et al., 2010). Samples (100–250 mg) were subject to a decalcification solution, 2 ml of 0.5 M EDTA solution, kept at room temperature for two days. They were then centrifuged for two minutes at 4000 g and supernatant removed. Samples were then rotated overnight at room temperature with 5 ml extraction buffer (0.5 M EDTA and 0.25 mg/ml proteinase K, pH 8.0). The following day samples were spun down for two minutes at 4000 g. Supernatant was decanted and added to 2.5 ml binding buffer (5M GuSCN, 25 mM NaCl and 50 mM Tris) and 100 μ l silica suspension as per Rohland et al. (2010). Samples were rotated at room temperature for three hours, and subsequently centrifuged for 2 min at 4000 g. Supernatant was discarded, and the silica pellet resuspended in 1 ml binding buffer and transferred to 1.7 ml mini-centrifuge tube. Samples were spun for 10 s at 16,000 g, and supernatant was discarded. The silica pellet was resuspended in 1 ml washing buffer (50% v/v ethanol, 125 mM NaCl, 10 mM Tris and 1 mM EDTA, pH 8.0). This washing step was repeated twice. After the final washing step, all liquid was removed and samples were allowed to air dry, with caps open for 15 min. Silica pellets were then resuspended in 50 μ l TE, and allowed to sit for 10 min at room temperature. Samples were centrifuged for two minutes at 16,000 g, and final elutate was transferred to a fresh tube. Elution steps were repeated, and both elutates were combined for a total volume of 100 μ l. All samples were extracted twice, in the VGL ancient DNA laboratory (with several months between primary extractions) and sequenced independently (described below). The canine pendant (BELA-00115-37940) was only extracted once, to minimize damage to this artifact. Modern Greenland and Inuit Sled Dog buccal swab samples extracted as per Oberbauer et al. (2003).

2.2. Polymerase chain reaction

Due to the fragmented nature of ancient DNA, we utilized multiple primer sets that amplified \sim 200 base-pair (bp) fragments (overlapping by 30 bp) a piece. In total a \sim 370 bp portion of the Hyper-variable1 region of the D-loop of Mitochondrial DNA was amplified with the following primers: HV1C2-F (CTTAATCACC ATGCCTCGAGA), HV1C2-R (GTTTCTTTTATGTGTGATCATGGGCTGA), HV1B2-F (CCCTCCCCTATGTACGTCG), and HV1B2-R (GTTTCTT GTTCTCGAGGCATGGTGAT) (primers developed by B. Wictum from the VGL Forensics Laboratory). Samples and extraction blanks (one per batch of 9 extractions) were amplified via Polymerase Chain Reaction (PCR), carried out in a volume of 25 μ l, consisting of: 3 μ l DNA extract, 1 \times PCR buffer, 3 mM MgCl₂, 0.2 mM dNTPs, 2.2 μ g/ μ l BSA, 0.5 μ m of each primer and 1 U of Amplitaq Gold (Applied Biosystems). Amplification was performed in an ABI 2720 thermal cycler. Conditions were set at; 94 C for 10 min, followed by 40 cycles of 94 C for 45 s, 50 C for 45 s and 72 C for 45 s; followed by 10 min of extension at 72 C. Although it has been standard in aDNA work to clone samples as a means of replication, this method is highly susceptible to base-misincorporations, whereas independent PCR reactions provide a more robust means of verifying sequences (Winters et al., 2011). Therefore, samples that yielded DNA in the initial amplification attempt were sequenced (forward and reverse strands of both amplicons) and then re-extracted, re-amplified and re-sequenced at least one additional time. Sequences were validated by aligning all sequences per individual to check for any errors. Amplicons of HV1B and HV1C were sequenced with Big Dye v 3.1 chemistry on an ABI 3730 capillary sequencer. Sequences were aligned with dog sequences from Genbank (Leonard et al., 2002; Pang et al., 2009; Savolainen et al., 2002), and then viewed in DNACollapser (Villesen, 2007) to obtain haplotype identification. Modern Greenland and Inuit Sled Dogs were amplified in one longer fragment using primers from Savolainen et al. (2002) and the above reaction conditions.

3. Results

We successfully amplified and sequenced 23 of the 28 archaeological and surface-find samples, yielding an overall success rate of 82.1% (Table 3). None of the extraction or PCR blanks yielded amplified DNA. All sequences were confirmed both through forward and reverse sequencing and through replicate extractions, PCR and sequencing reactions, resulting in 368–371 bp (depending on indels) sequences with only one sample that contained base ambiguities. Sample KNK492x37 had a single C to T deamination in one out of three sequences in the forward direction of the B amplicon. Nevertheless, because we only sequenced \sim 370 bases, some sequences were consistent with >1 previously described 582 bp haplotype. Twenty of the archaeological samples matched Genbank-accessioned sequences of dog based on Basic Local Alignment Search Tool (BLAST), while three samples exhibited a novel haplotype (Genbank No. JX185398) that aligned most closely with gray wolf (*Canis lupus*) sequences, for example, differing by one substitution from Genbank No. AB499820.1. In contrast, the most similar dog haplotype was HQ452419.1, which differed by three substitutions. The canine pendant artifact (BELA-00115-37940) was sequenced for 185 bp (extracted once to reduce damage to the artifact), and matched the novel wolf haplotype (Genbank No. JX185398) for all base pairs sequenced. Additionally, osteological measurements associated with these two mandibles and one maxillary canine pendant are entirely consistent with wolf. Their size is considerably larger than any of the adult dog remains (see Appendix A), all of which are consistent with a large variety of dog (Crockford, 1997).

Table 3

Canis specimens sampled ($n = 28$) and amplified for mtDNA ($n = 23$) from western Alaska and northwestern Greenland; organized by geographic locality and time period. Unless otherwise noted, haplotype names (following nomenclature of Savolainen et al., 2002) indicate the only 582 bp sequence consistent with the shorter fragments sequenced in this study.

Specimen #	Location	Time period	Context	Skeletal element	Species (BLAST)	Fragment length	Haplotype name
BELA-00112-36034	Alaska	ca. AD 1260–1400	Pre-contact	Premolar	<i>C. l. familiaris</i>	370 bp	A31
BELA-00112-36035	Alaska	ca. AD 1260–1400	Pre-contact	Premolar	<i>C. l. familiaris</i>	370 bp	A31
BELA-00112-37373	Alaska	ca. AD 1260–1400	Pre-contact	Premolar	<i>C. l. lupus</i>	368 bp	(Gray wolf) ^a
BELA-00112-37374	Alaska	ca. AD 1260–1400	Pre-contact	Premolar	<i>C. l. familiaris</i>	370 bp	A121
BELA-00112-37375	Alaska	ca. AD 1260–1400	Pre-contact	Premolar	<i>C. l. familiaris</i>	371 bp	A29 ^b
BELA-00112-37376	Alaska	ca. AD 1260–1400	Pre-contact	Premolar	<i>C. l. familiaris</i>	367 bp	A29 ^b
BELA-00109-35135	Alaska	ca. AD 1275–1450	Pre-contact	Calcaneus	No results	No results	No results
BELA-00115-37940	Alaska	ca. AD 1275–1450	Pre-contact	Canine	<i>C. l. lupus</i>	185 bp	(Gray wolf)
BELA-00112-37370	Alaska	ca. AD 1450–1650	Pre-contact	Premolar	<i>C. l. familiaris</i>	370 bp	A31
BELA-00112-37371	Alaska	ca. AD 1450–1650	Pre-contact	Premolar	<i>C. l. lupus</i>	368 bp	(Gray wolf) ^a
BELA-00112-37367	Alaska	ca. AD 1675–1800	Pre-contact	Ulna	No results	No results	No results
BELA-00112-37368	Alaska	ca. AD 1675–1800	Pre-contact	Ulna	No results	No results	No results
BELA-00112-37369	Alaska	ca. AD 1675–1800	Pre-contact	Ulna	<i>C. l. familiaris</i>	371 bp	A29 ^b
KNK492-36	Greenland	ca. AD 1275–1440	Pre-contact	Premolar	<i>C. l. familiaris</i>	370 bp	A31
KNK492-37	Greenland	ca. AD 1275–1440	Pre-contact	Premolar	<i>C. l. familiaris</i>	370 bp	A31
KNK492-38	Greenland	ca. AD 1275–1440	Pre-contact	Premolar	<i>C. l. familiaris</i>	370 bp	A31
KNK492-39	Greenland	ca. AD 1275–1440	Pre-contact	Mandible	No results	No results	No results
KNK494-1	Greenland	ca. AD 1275–1440	Pre-contact	Incisor	<i>C. l. familiaris</i>	370 bp	A31
KNK494-2	Greenland	ca. AD 1275–1440	Pre-contact	Incisor	<i>C. l. familiaris</i>	370 bp	A31
KNK494-3	Greenland	ca. AD 1275–1440	Pre-contact	Premolar	<i>C. l. familiaris</i>	370 bp	A31
KNK2643-1838	Greenland	ca. AD 1275–1650	Pre-contact	Premolar	No results	No results	No results
KNK2644-1119	Greenland	ca. AD 1850–1900	Post-contact	Premolar	<i>C. l. familiaris</i>	370 bp	A11
KNK2644-1120	Greenland	ca. AD 1850–1900	Post-contact	Premolar	<i>C. l. familiaris</i>	370 bp	A31
KNK2644-1121	Greenland	ca. AD 1850–1900	Post-contact	Premolar	<i>C. l. familiaris</i>	370 bp	A31
KNK2643-1839	Greenland	ca. AD 1900–1910	Post-contact	Premolar	<i>C. l. familiaris</i>	370 bp	A31
UCDZL-1081 ^c	Greenland	ca. AD 1930–1990	Post-contact	Nasal turbinates	<i>C. l. familiaris</i>	370 bp	A31
UCDZL-1082 ^c	Greenland	ca. AD 1930–1990	Post-contact	Nasal turbinates	<i>C. l. familiaris</i>	370 bp	A18/A20 ^d
UCDZL-1080 ^c	Greenland	ca. AD 1980–1990	Post-contact	Nasal turbinates	<i>C. l. familiaris</i>	370 bp	A31

^a Gray wolf Genbank accession No. JX185398. BELA-00115-37940 matches this haplotype for all 185 bp sequenced.

^b These sequences were also consistent with the following rare 582 bp haplotypes: A49, A58, A60, A43, A179, or A180 (Savolainen et al., 2002).

^c Surface find.

^d This sequence was also consistent with the 582 bp haplotype A94 found in a single dog in Hunan, China (Savolainen et al., 2002).

Otherwise, the 20 dog sequences reflected five distinct haplotypes exhibiting an overall haplotype diversity of 0.48. Most of the samples possessed haplotype A31, including nine of the 13 pre-contact samples (69.2%) and five of the seven post-contact samples (71.4%); the frequencies associated with the two time periods were statistically indistinguishable (Fisher Exact test, $P = 0.39$). The remaining six samples possessed haplotypes A11, A121, and two additional haplotypes, most likely A29 and A18/A20 (although each was also consistent with additional rare 582 bp haplotypes; Table 3 and 4).

The 51 modern Inuit Sled Dogs possessed six haplotypes with a combined haplotype diversity of 0.35 ± 0.08 . As with the pre-contact sample, the haplotype with the highest frequency was A31 (41 out of 51 individuals; 80.4%) and its frequency did not differ significantly between the modern and pre-contact samples (Fisher Exact test, $P = 0.12$). Five additional haplotypes were present, including A29, A49, A20, A181, and a novel haplotype (Genbank No. JX185397) differing by one substitution from A18 (Table 4). These haplotypes were either previously found only in Inuit Sled Dogs (A31 and A181; Klütsch et al., 2010; Savolainen et al., 2002), found

Table 4

Mitochondrial DNA haplotypes and number of individuals identified from our analysis of modern Inuit Sled Dogs from the Veterinary Genetics Laboratory (582 bp haplotypes), and from pre-contact archaeological and post-contact archaeological/surface-find dog bone and tooth specimens from Alaska and Greenland (~370 bp haplotypes).

Haplotype	Pre-contact archaeological	Post-contact archaeological/surface	Modern Inuit Sled Dog	Total	%	Comments
A11	0	1	0	1	1.4	Universal type, identified in modern and ancient dogs (Leonard et al., 2002)
Novel (JX185397)	0	0	1	1	1.4	Closest to A18 – Universal type
A18/A20	0	1 ^a	4	5	7.0	Universal type, but not identified in any other spitz-type northern dogs; must be ancient haplotype. Identified in dogs from Vietnam, Pharaoh hounds, Anatolians, and Portuguese water dogs
A29	3 ^b	0	3	6	8.5	Widespread in East Asia and ancient North America (Leonard et al., 2002; Barta, 2007)
A31 ^c	9	5	41	55	77.5	Identified only in Canadian Inuit or Greenland sled dogs
A49	0	0	1	1	1.4	Identified in Finish Laika; indel off from A49 found in West Siberian and Russian Laikas, and Karelian Bear dogs
A121	1	0	0	1	1.4	Identified only in dogs from China and Vietnam
A181 ^c	0	0	1	1	1.4	Identified in only one other study; from an Inuit dog (Klütsch et al., 2010)
Total	13	7	51	71	100.0	

^a This sequence also consistent with the 582 bp haplotype A94 found in a single dog in Hunan, China (Savolainen et al., 2002).

^b These sequences also consistent with rare haplotypes A43, A49, A58, A60, A179, and A180.

^c Novel Arctic haplotype.

throughout the world (A20), found solely in East Asia (and Australian and New Guinean dingoes) and pre-contact North American dogs (A29/A49) (Barta, 2007; Leonard et al., 2002), or were novel. Additionally, a survey of published modern arctic dogs (Klüttsch et al., 2010) revealed, similarly to our findings, a high frequency of haplotype A31 in Inuit Sled Dogs (63.5%) but a comparably low frequency (3.8%) of this haplotype in Alaskan Malamutes (Table 5). More generally, the contrast in haplotype frequencies of modern malamutes with all ancient Arctic dogs and with modern Eastern Arctic dogs suggests near total replacement in the Western Arctic in recent times (Tables 4 and 5).

4. Discussion

Studies utilizing ancient DNA have revealed that the genetic composition of haplotypes in dog populations throughout much of the Americas and even Europe have changed dramatically over a few thousand to even just a few hundred years (Barta, 2007; Castroviejo-Fisher et al., 2011; Deguilloux et al., 2008; Leonard et al., 2002; Malmström et al., 2008). Such lineage replacement has taken place through the introduction of modern, primarily European breeds. In the present study, we utilized ancient and modern DNA of dogs in the Greenland and Alaskan Arctic to determine 1) if the haplotypes observed there in the present population were indigenous, 2) whether these same haplotypes were found in the western Arctic prior to European intervention in racing sled-dog breeding, and 3) whether Western breed genes have substantially penetrated Inuit Sled Dog populations. We successfully sequenced 20 archaeological (ca. 800–200 B.P.) and three surface-collected modern *Canis* bone and tooth samples, and compared them to 51 modern Inuit Sled Dogs to test for evidence of lineage replacement or genetic continuity through time. Our sequencing efforts revealed haplotype A31 (Savolainen et al., 2002), a type unique to Arctic dogs, to be a common thread tying our archaeological and modern eastern Arctic breed dogs together. It seems likely that the remote and relatively isolated nature of Greenland has contributed to the preservation of indigenous dogs in the East Arctic, thus adding another population to those of East Asia, parts of Africa, Australia, Island Southeast Asia, and the Middle East, whose DNA retains information about Neolithic migrations (Brown et al., 2011).

In addition to detecting genetic continuity through time, we also detected genetic continuity over geography. Our archaeological samples included individuals carrying haplotype A31 both from Greenland ($n = 9$) and Alaska ($n = 3$). This finding is significant in its application to human migrations. It is well known that the language

spoken from northern Alaska to Arctic Canada and Greenland is part of the Inuktitut language family. Archaeologists have long noted the material culture connection across this region (e.g., Giddings, 1967; Mathiassen, 1927; Maxwell, 1985) and numerous studies of Arctic genetics has provided additional support for the migration (e.g., Crawford, 2007; Hayes et al., 2003, 2005; Helgason et al., 2006). With further pre-contact sampling throughout Alaska, Canada, and Greenland, we could use the presence of haplotype A31 as a proxy for human migrations, as has been done with other commensal animals (Matisoo-Smith and Robins, 2004; Searle et al., 2009).

Our pre-contact dogs possessed three definitively identifiable haplotypes, the high-frequency, geographically restricted A31 (Savolainen et al., 2002), A121 (Pang et al., 2009), and a Universal Type (A11), that occurs world-wide (and was found in pre- and post-contact dogs from Fairbanks, Alaska; Leonard et al., 2002) and therefore is most likely an ancient haplotype (Pang et al., 2009). Additionally, four samples had two other haplotypes, most likely A29 (also found in our modern Inuit Sled Dogs) and A18 or A20 (both Universal Types). Our survey of 51 Inuit Sled Dogs turned up three additional haplotypes in low frequency, at least two of which were likely indigenous. The A181 haplotype found in one modern dog, previously found only in another modern Inuit Sled Dog, was derived from the indigenous A31 haplotype (Klüttsch et al., 2010). Another was novel, also consistent with being indigenous. It is possible that the remaining haplotype found in one of the modern dogs (A49, previously found in Scandinavian and Siberian dogs) reflects an introduced haplotype. Regardless, the similar frequencies of A31, A20, and A29 in the two temporal samples of Eastern Arctic dogs suggest that the majority if not all of the matrilineal ancestry of today's dogs is indigenous. Interestingly, the pre-contact haplotypes (A121) discovered in one individual (BELA-00112-37374) from the earliest house tested at Cape Espenberg, Alaska had previously been identified only in three modern dogs from Vietnam and southern China (Guangxi), consistent with the hypothesis of a major expansion of dogs from this region (Savolainen et al., 2002; Pang et al., 2009).

This study, albeit preliminary, offers insights into both dog and human history. We have demonstrated a North American dog population with a genetic signature that appears to be relatively unchanged for at least the past 700 years. With further research we will be able to more readily determine the origin of Arctic dogs, which could yield to further insights on Neolithic human-dog co-migrations. In particular, with broadened sampling, both in time (e.g., Paleoeskimo dogs from the Eastern Arctic) and geography, we can use these dogs as a proxy for human movement and interaction across the Arctic and with adjacent regions. In addition, expanded sequencing of the mitochondrial genome, e.g., associated with "A29" and "A31" haplotypes, and typing of Y STRs (Brown et al., 2011) can elucidate timing of interchange across continents. For example, recent findings of a cast bronze artifact from Cape Espenberg (where we found the A121 haplotype) supports a late-Holocene Asian connection (CU Boulder News Release, 2011). Finally, further testing of samples from ancient samples from East Asia may yield further insight into the nature of continental interchange.

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Table 5
Mitochondrial DNA haplotypes (582 bp) previously identified from modern Arctic dog breeds (Klüttsch et al., 2010; Pang et al., 2009). Bolded numbers indicate the haplotype with the highest frequency in both breeds.

Haplotype	Alaskan Malamute	%	Inuit Sled Dog	%
A2	–	–	1	1.9
A11	5	19.2	3	5.8
A17	2	7.7	1	1.9
A18	3	11.5	2	3.8
A20	–	–	8	15.4
A29	12	46.2	–	–
A31	1	3.8	33	63.5
A63	–	–	1	1.9
A124	–	–	2	3.8
A156	1	3.8	–	–
A179	2	7.7	–	–
A181	–	–	1	1.9
Total	26	100.0	52	100.0

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jas.2012.09.010>.

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