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RESEARCH ARTICLE SUMMARY

ARCTIC GENETICS

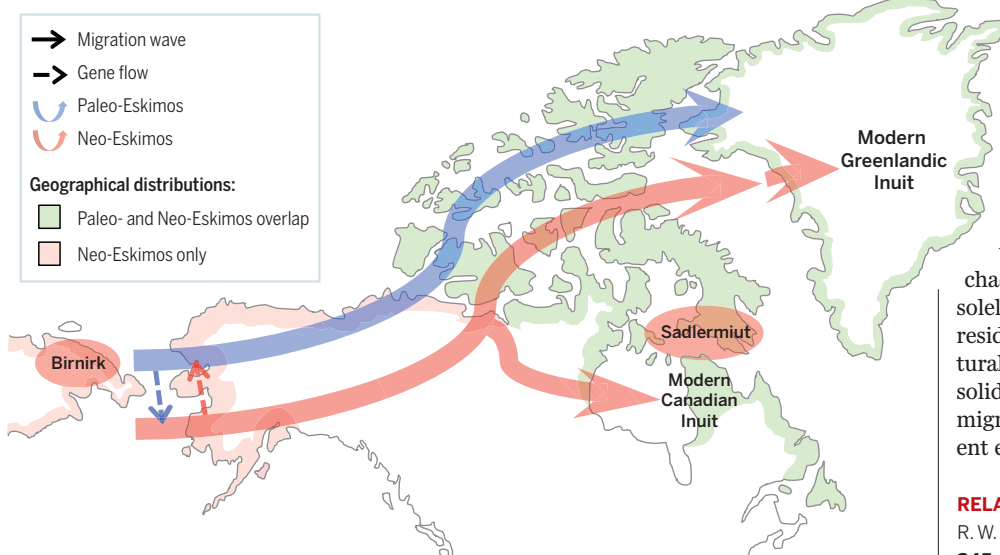
The genetic prehistory of the New World Arctic

Maanasa Raghavan, Michael DeGiorgio, Anders Albrechtsen, Ida Moltke, Pontus Skoglund, Thorfinn S. Korneliusen, Bjarne Grønnow, Martin Appelt, Hans Christian Gulløv, T. Max Friesen, William Fitzhugh, Helena Malmström, Simon Rasmussen, Jesper Olsen, Linea Melchior, Benjamin T. Fuller, Simon M. Fahrni, Thomas Stafford Jr., Vaughan Grimes, M. A. Priscilla Renouf, Jerome Cybulski, Niels Lynnerup, Marta Mirazon Lahr, Kate Britton, Rick Knecht, Jette Arneborg, Mait Metspalu, Omar E. Cornejo, Anna-Sapfo Malaspinas, Yong Wang, Morten Rasmussen, Vibha Raghavan, Thomas V. O. Hansen, Elza Khusnutdinova, Tracey Pierre, Kirill Dneprovsky, Claus Andreasen, Hans Lange, M. Geoffrey Hayes, Joan Coltrain, Victor A. Spitsyn, Anders Götherström, Ludovic Orlando, Toomas Kivisild, Richard Villems, Michael H. Crawford, Finn C. Nielsen, Jørgen Dissing, Jan Heinemeier, Morten Meldgaard, Carlos Bustamante, Dennis H. O'Rourke, Mattias Jakobsson, M. Thomas P. Gilbert, Rasmus Nielsen, Eske Willerslev*

INTRODUCTION: Humans first peopled the North American Arctic (northern Alaska, Canada, and Greenland) around 6000 years ago, leaving behind a complex archaeological record that consisted of different cultural units and distinct ways of life, including the Early Paleo-Eskimos (Pre-Dorset/Saqqaq), the Late Paleo-Eskimos (Early Dorset, Middle Dorset, and Late Dorset), and the Thule cultures.

RATIONALE: We addressed the genetic origins and relationships of the various New World Arctic cultures to each other and to

modern-day populations in the region. We obtained 26 genome-wide sequences and 169 mitochondrial DNA sequences from ancient human bone, teeth, and hair samples from Arctic Siberia, Alaska, Canada, and Greenland, and high-coverage genomes of two present-day Greenlandic Inuit, two Siberian Nivkhs, one Aleutian Islander, and two Athabascan Native Americans. Twenty-seven ancient samples were radiocarbon dated for accurate cultural assignment, of which 25 were corrected for marine reservoir effect to account for the dominant marine component in these individuals' diets.



Genetic origins of Paleo-Eskimos and Neo-Eskimos. All Paleo-Eskimos represent a single migration pulse from Siberia into the Americas, independent of the Neo-Eskimo Thule people (ancestors of modern-day Inuit) and the related extinct Sadlermiut population. The Siberian Birnirk people were likely cultural and genetic ancestors of modern-day Inuit. We also show ancient admixture between the Paleo- and Neo-Eskimo lineages, occurring at least 4000 years ago.

RESULTS: Nuclear and mitochondrial DNA data unequivocally show that the Paleo-Eskimos are closer to each other than to any other present-day population. The Thule culture represents a distinct people that are genetic and cultural ancestors of modern-day Inuit. We additionally find the Siberian Birnirk culture (6th to 7th century CE) as likely cultural and genetic ancestors of the Thule. The extinct Sadlermiut people from the Hudson Bay region (15th to 19th century CE), considered to be Dorset remnants, are genetically closely related to Thule/Inuit, rather than the Paleo-Eskimos. Moreover,

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there is no evidence of matrilineal gene flow between Dorset or Thule groups with neighboring Norse (Vikings) populations settling in the Arctic around 1000 years ago. However, we do detect gene flow between the Paleo-Eskimo and Neo-Eskimo lineages, dating back to at least 4000 years.

CONCLUSION: Our study has a number of important implications: Paleo-Eskimos likely represent a single migration pulse into the Americas from Siberia, separate from the ones giving rise to the Inuit and other Native Americans, including Athabascan speakers. Paleo-Eskimos, despite showing cultural differences across time and space, constituted a single population displaying genetic continuity for more than 4000 years. On the contrary, the Thule people, ancestors of contemporary Inuit, represent a population replacement of the Paleo-Eskimos that

occurred less than 700 years ago. The long-term genetic continuity of the Paleo-Eskimo gene pool and lack of evidence of Native American admixture suggest that the Saqqaq and Dorset people were largely living in genetic isolation after entering the New World. Thus, the Paleo-Eskimo technological innovations and changes through time, as evident from the archaeological record, seem to have occurred solely by movement of ideas within a single resident population. This suggests that cultural similarities and differences are not solid proxies for population movements and migrations into new and dramatically different environments, as is often assumed. ■

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RESEARCH ARTICLE

ARCTIC GENETICS

The genetic prehistory of the New World Arctic

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The New World Arctic, the last region of the Americas to be populated by humans, has a relatively well-researched archaeology, but an understanding of its genetic history is lacking. We present genome-wide sequence data from ancient and present-day humans from Greenland, Arctic Canada, Alaska, Aleutian Islands, and Siberia. We show that Paleo-Eskimos (~3000 BCE to 1300 CE) represent a migration pulse into the Americas independent of both Native American and Inuit expansions. Furthermore, the genetic continuity characterizing the Paleo-Eskimo period was interrupted by the arrival of a new population, representing the ancestors of present-day Inuit, with evidence of past gene flow between these lineages. Despite periodic abandonment of major Arctic regions, a single Paleo-Eskimo metapopulation likely survived in near-isolation for more than 4000 years, only to vanish around 700 years ago.

Humans first peopled the North American Arctic (northern Alaska, Canada, and Greenland) from the Bering Strait region beginning around 6000 years before the present (1), leaving behind a complex archaeological record [supplementary text S1 (2) and Fig. 1]. Over successive millennia, the pioneering Arctic cultures developed into distinct lifestyles and cultural stages grouped within two broad cultural traditions known as Paleo-Eskimo and Neo-Eskimo. Early Paleo-Eskimo people representing the Denbigh, Pre-Dorset, Independence I, and Saqqaq cultures (~3000 to 800 BCE) lived in tent camps and hunted caribou, musk ox, and seals with exquisitely flaked stone tools similar to those used by northeast Siberian Neolithic cultures (3–6). In northern Alaska, the Denbigh cultural groups were succeeded by the Paleo-Eskimo Choris and Norton cultures starting around 900 BCE, with the Norton material culture further developing into the Ipiutak culture around 200 CE (6, 7). Simultaneously, during the cold period beginning around 800 BCE, innovations in housing and hunting technologies accompanied the formation of the Late Paleo-Eskimo or Dorset culture in eastern Arctic (eastern Canadian Arctic and Greenland), with population growth

and more intensive use of marine mammals, including walrus (8, 9). The Dorset culture is divided into three phases: (i) Early Dorset, ~800 BCE to 0 BCE/CE; (ii) Middle Dorset, ~0 BCE/CE to 600 to 800 CE; and (iii) Late Dorset ~600 to 800 CE to 1300 CE (9). The Paleo-Eskimo tradition in the eastern Arctic ended sometime between 1150 to 1350 CE, shortly after the sudden appearance of the Neo-Eskimo Thule whale-hunters from the Bering Strait region (9–17).

The Siberian Old Bering Sea culture is the earliest expression of the Neo-Eskimo tradition ~2200 years before the present, developing into the Penuk culture around the sixth century CE. Almost concurrently, the Old Bering Sea culture developed into the Birnirk culture in the northern parts of the Bering Strait region. Interactions between people of the Birnirk and Penuk cultures gave rise to the western Thule culture on both sides of the Bering Strait, with contribution from the Paleo-Eskimo Ipiutak culture in Alaska (18). By the early second millennium CE, western Thule cultural groups began their movement into the eastern North American Arctic (14, 19). With the Thule culture came more effective means of transportation like dog sleds and large skin boats, complex tool kits like sinew-backed bows,

and harpoon float gear for hunting large whales (10, 20). Thule culture spread quickly throughout the eastern Arctic, rapidly replacing Dorset in most, if not all, regions. The decline of whaling during the latter part of the Little Ice Age (16th to 19th century CE) resulted in a readjustment to ice-edge hunting of walrus and breathing-hole

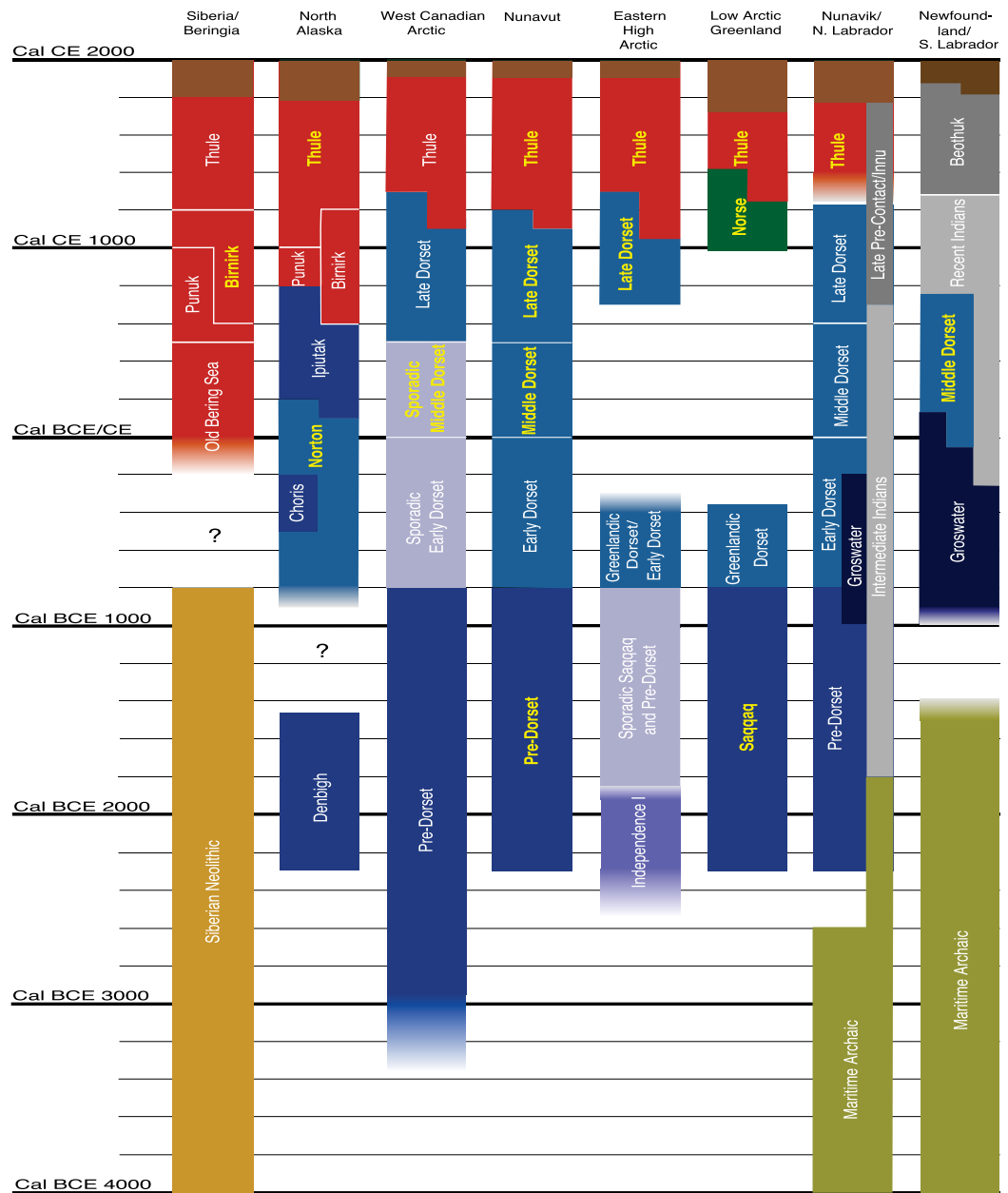
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Fig. 1. Chronology of the prehistoric cultures in the New World Arctic and northeast Siberia.

This framework is based on a combination of screened radiocarbon dates on associated terrestrial materials, typological studies, and contexts [e.g., (6, 9, 37, 40, 83–85)]. Fading colors symbolize uncertainties concerning the beginnings or ends of the archaeological cultures, owing to plateaus or wiggles in the radiocarbon calibration curve or lack of data. Defined archaeological phases within a culture are separated by a white line. Dark reddish-brown toward the top of the figure indicates historical times from which samples included in this study arise are highlighted in yellow.



hunting of seal, laying the foundation for modern Inuit cultures (21). Additionally, the Norse (Vikings) formed settlements in Greenland around 985 CE and occupied regions in southern Greenland for about 500 years, contemporaneous with both the Late Dorset and Thule, reaching Newfoundland and Labrador in eastern Canada around 1000 CE (22).

Continuities in chipped stone bifaces and blade and burin technology point to Paleo-Eskimo origins among Siberian Neolithic cultures (6, 10, 23, 24). Genetic evidence suggests that the earliest eastern Arctic Paleo-Eskimo people represented an independent Siberian migration into the New World (25, 26) (Fig. 2B, scenario 1). However, to date, we have been unable to identify the likely Siberian ancestral population. Some have argued for origins from an ill-defined 8000-year-old South

Alaskan Eskimo-Aleut or Na Dene blade and burin complex (27), but this remains controversial. A recent genetic study provides evidence in support of the Early Paleo-Eskimos, specifically Saqqaq, sharing ancestry with Na Dene Native Americans (Fig. 2B, scenario 2), as part of a three-wave peopling model of the Americas consisting of (i) First Americans, (ii) Eskimo-Aleuts and, (iii) Saqqaq and Na Dene speakers (28). Alternative hypotheses on Dorset origins include the Aleutian Islanders (29) (Fig. 2B, scenario 3) and earlier theories of Amerindian cultures in eastern Canada and even further south (30–33) (Fig. 2B, scenario 4). Current views favor an in situ origin of Dorset from Canadian Pre-Dorset in northern Hudson Bay (10, 13, 34, 35).

Additionally, whether the individual Early, Middle, and Late Dorset phases represent genetic

continuity of the same peoples or not remains unresolved (Fig. 2A). The Dorset chronological sequence from the T1 site on Southampton Island, Igloolik, South Baffin, and Labrador in Canada provide evidence of cultural continuity through Early to Late Dorset (20, 30, 36), although regional differences and settlement discontinuities are also common (37–41). Notable regional discontinuities and occupation gaps also occur in Greenland (9). It is also debated whether abandoned areas were reoccupied by people from a different genetic background and whether this occurred from a Central Arctic ecological “core area” or regional “core areas” into which human populations retreated and restructured before expanding again into periodically refurbished marginal zones (20, 34). The resolution of these controversies has been hindered by the limited

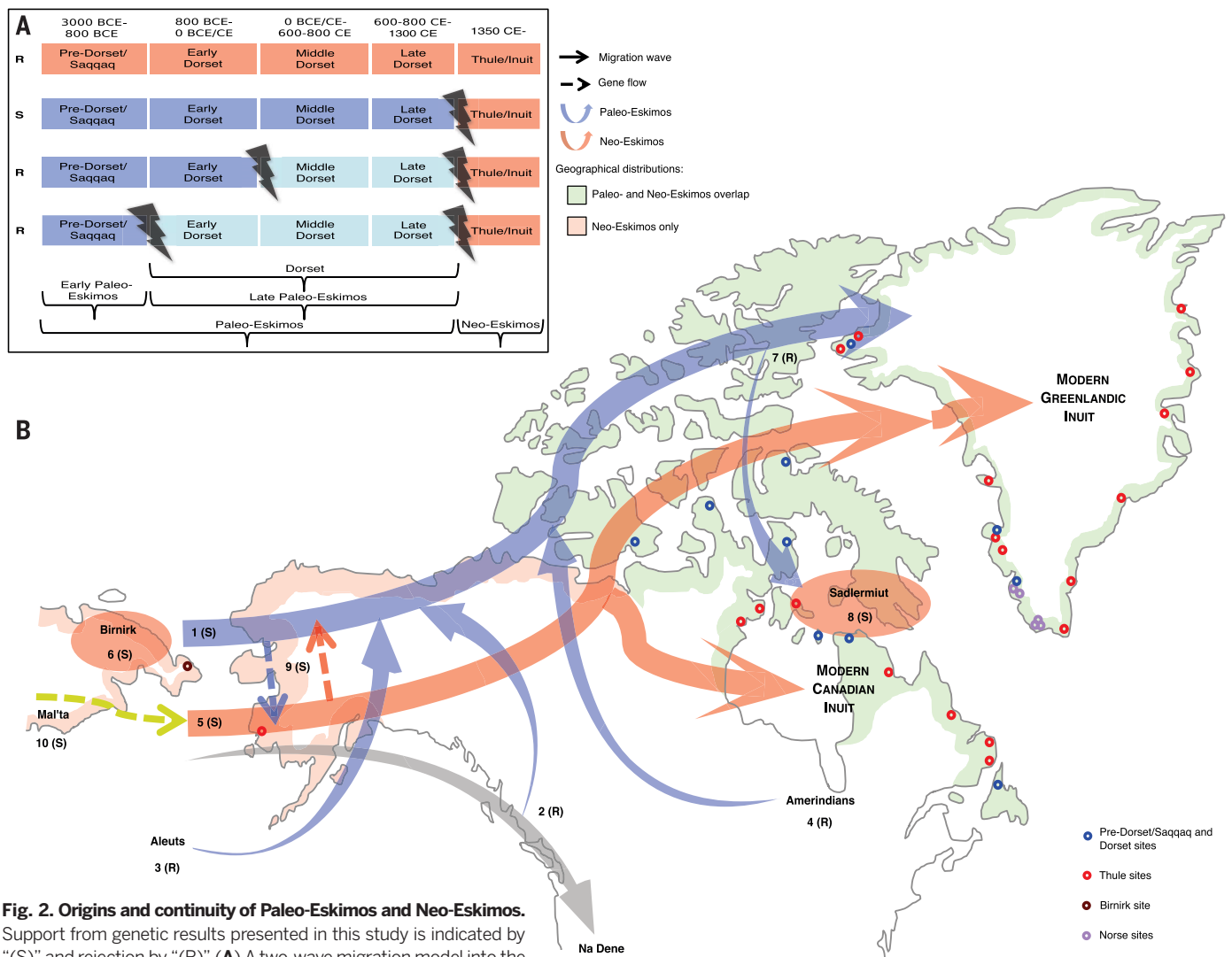


Fig. 2. Origins and continuity of Paleo-Eskimos and Neo-Eskimos.

Support from genetic results presented in this study is indicated by “(S)” and rejection by “(R)”: (A) A two-wave migration model into the New World Arctic, with continuity throughout the Paleo-Eskimo tradition, followed by the Neo-Eskimo migration, is supported. Black thunderbolt symbols represent genetic discontinuity. (B) This schematic summarizes the origins of Paleo- and Neo-Eskimos in the archaeological and genetic literature, including the present study, and their relationships with other ancient populations in the North American Arctic. See main text for details on the different scenarios represented by numbers 1 to 10 in the figure. For reference, we show the maximal geographical distribution of the Paleo-Eskimos and Neo-Eskimos in the New World Arctic and far-east Siberia (9). Additionally, plotted are Paleo-Eskimo (Pre-Dorset, Saqqaq, Dorset), Thule, Birnirk, and Norse sites from which samples in this study derive; for further information, see fig. S1 and table S1.

amount of Paleo-Eskimo human material, difficulties in assigning cultural affiliation of some finds (41), and dating uncertainties resulting from the strong marine component in the Arctic diet (9).

Samples and sequence data

We collected bone, teeth, and hair samples from the field and museums representing 169 ancient human remains from Arctic Siberia, Alaska, Canada, and Greenland (fig. S1 and table S1). These remains have been assigned to one of several ancient Arctic cultures on the basis of typological and/or stratigraphic evidence and, in some cases, radiocarbon dating (supplementary text S1). To circumvent drawing conclusions from single genomes (42), we generated mitochondrial DNA (mtDNA) data from 154 and low-coverage whole genome data sets from 26 of the ancient samples

(up to 0.3× depth) (supplementary text S3 and tables S1 and S7). Despite colder temperatures in the Arctic, DNA survival in the ancient samples was surprisingly low, ranging from ~0 to 3.2% endogenous content based on the genome sequencing data (table S7). This low endogenous content may be explained by the remains being largely surface burials that suffered from fluctuating temperatures and humidity, and to subsequent storage conditions at museums.

We also sequenced two high-coverage genomes from present-day North American Native Americans belonging to the Na Dene family (the Dakelh of British Columbia, hereafter referred to as Athabascans) and unrelated, present-day Greenlandic Inuit ($n = 2$), Aleutian Islander ($n = 1$) and Siberian Nivkhs ($n = 2$) to average depths of 20 to 40× (supplementary text S3 and table S8). Only the Aleutian Islander showed evidence of recent

European admixture and was masked for non-Native American ancestry tracts prior to analyses (supplementary text S5). Additionally, we radiocarbon dated 27 ancient samples and corrected 25 of the dates for marine reservoir effect to account for the dominant marine component in these individuals' diets (15 of these samples are represented in the ancient genomic data set) (supplementary text S2). This is critical in the accurate cultural assignment of these individuals, especially in cases where stratigraphic information is inconclusive or contentious (supplementary text S1).

Origins of Paleo-Eskimos

Diagnostic mtDNA coding region markers were targeted in the ancient samples to determine their mtDNA haplogroup (hg) affinities. Although hgs A, B, C, D, and X are the five founding mtDNA haplogroups in the Americas,

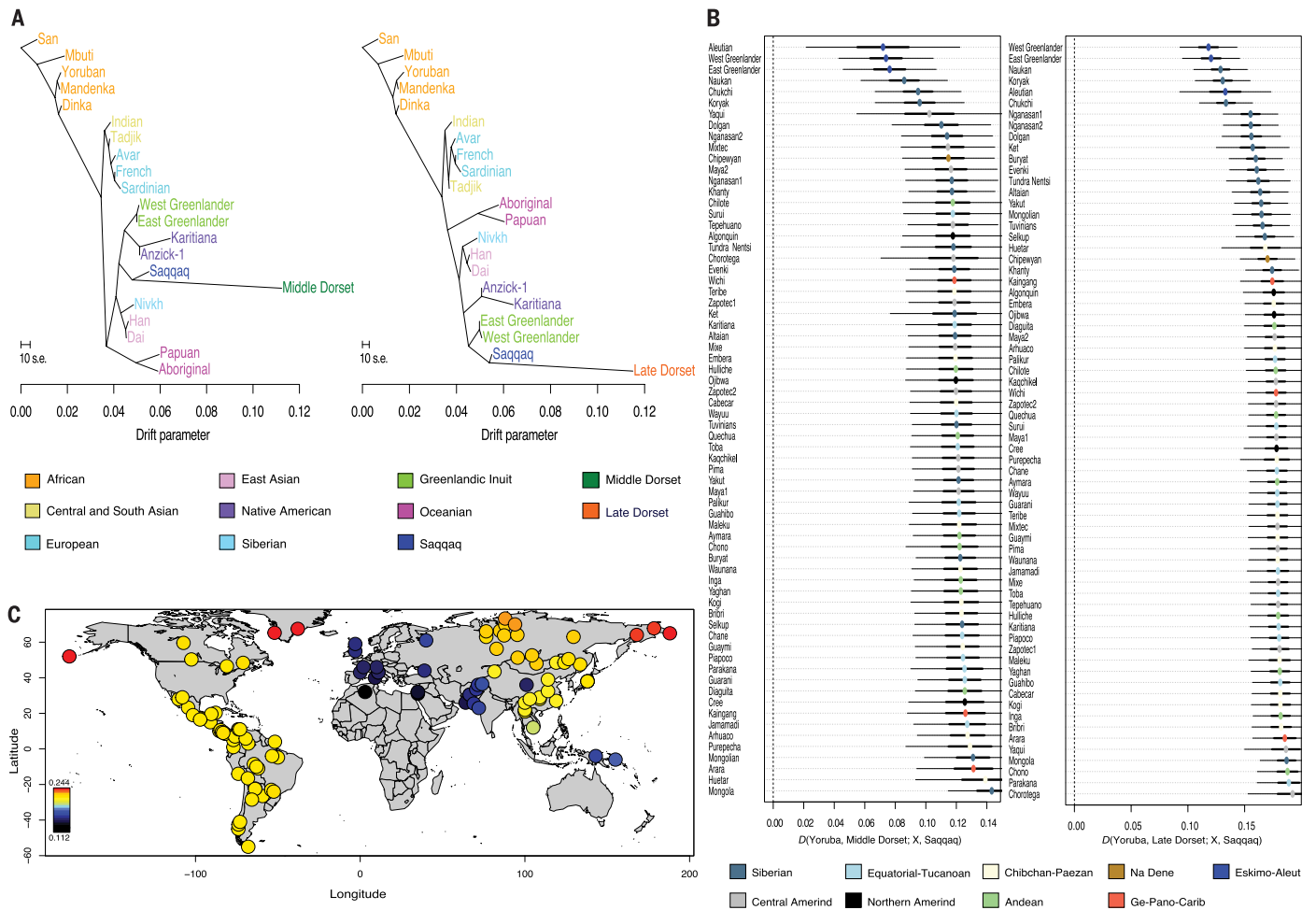


Fig. 3. Origins of Paleo-Eskimos and genetic continuity. (A) Sequencing data-based maximum likelihood trees constructed with *TreeMix* (51) with the high-coverage Saqqaq (26), Middle Dorset, and Late Dorset data sets, and 17 present-day and two ancient populations; for Greenlandic Inuit, see note in supplementary text S5. The scale bar represents 10 times the average standard error (s.e.) of the values in the covariance matrix. Residual matrices are shown in fig. S8, C and D. (B) SNP chip data-based D -statistic tests of the form $D(\text{Yoruba}, \text{Dorset}; X, \text{Saqqaq})$, where X represents present-day American and Siberian

populations from (28) (colored centers represent populations divided by linguistic affiliation, see legend at bottom). Thick and thin lines represent 1 and 3 standard errors of the D -statistics, respectively. Middle and Late Dorset (left and right panels, respectively) are significantly (no overlap at 3 standard errors) closer to Saqqaq than to the sampled present-day populations. (C) Heat map of the SNP chip data-based statistic $f_3(\text{Yoruba}; \text{Saqqaq}, X)$, where X represents present-day worldwide non-African populations from (28). The graded heat key (to the left of the image) represents the magnitude of the computed f_3 -statistics.

previous studies have shown the near-absence of hgs B, C, and X in Paleo-Eskimos and Thule, as well as among present-day Inuit (25, 43–47). We observe mtDNA hg D, specifically the lineage hg D2a, in both Early and Late Paleo-Eskimos, with the majority of the Pre-Dorset/Saqqaq and Middle Dorset samples further classified as hg D2a1 (supplementary text S4 and tables S1 and S9A). The absence of biological remains affiliated to the Early Dorset phase precludes genetic testing for this period. Hgs D2a and D2a1 are found in present-day Aleutian Islanders and Siberian Eskimos (48), who are genetical-ly among the closest living populations to the previously sequenced Greenlandic Paleo-Eskimo (Saqqaq) individual that also belonged to hg D2a1 (hereafter, high-coverage Saqqaq) (26). The single Canadian Pre-Dorset sample (XIV-H:168, Rocky Point) was typed to hg D4e [referred to as hg D2 in (48)], which is ancestral to hg D2a, but lacks further phylogenetic resolution owing to the low-

coverage nature of the shotgun data (supple-mentary text S4).

Maximum likelihood trees based on nuclear DNA variation place the Middle Dorset, Late Dorset, and the Canadian Pre-Dorset individuals as sister groups to the high-coverage Saqqaq individual (Fig. 3A and fig. S8, B to D), separately from contemporary Greenlandic Inuit or Native Americans [represented by the South American Karitiana (49) and the ancient Clovis Anzick-1 individual (50)]. Similar results were obtained when allowing for admixture between popula-tions with *TreeMix* (51) (fig. S8, C and D). When the analysis was repeated and included the Aleu-tian Islander, which was masked for European ancestry over ~80% of its genome (supplemen-tary text S5), the Middle Dorset and the Late Dorset individuals grouped with the high-coverage Saqqaq, as before (fig. S9).

Pairwise outgroup f_3 -statistics (52, 53) and D -statistics (52, 54) confirm Early and Late Paleo-

Eskimos as being significantly [no overlap at three standard errors for the single-nucleotide poly-morphism (SNP) chip data and at 1 standard error for the sequencing data] closer to one another than to any of the sampled present-day populations, including those from the Americas and Siberia (Fig. 3B and fig. S10, A to D). Fur-thermore, admixture clustering profiles (55) of the high-coverage Saqqaq and a Dorset indi-vidual are near-identical (fig. S7), with both sharing components with present-day Siberian Chukchi and Greenlandic Inuit and, to a lesser extent, with other Siberians and East Asians (Han). We note that variations in *TreeMix* graph topologies occurred with the inclusion of the different ancient samples (supplementary text S5); however, the resulting conclusions from these trees are consistent with other analyses. Hence, evidence from mitochondrial as well as nuclear markers suggests that all Paleo-Eskimos, from both Canada and Greenland, represent a

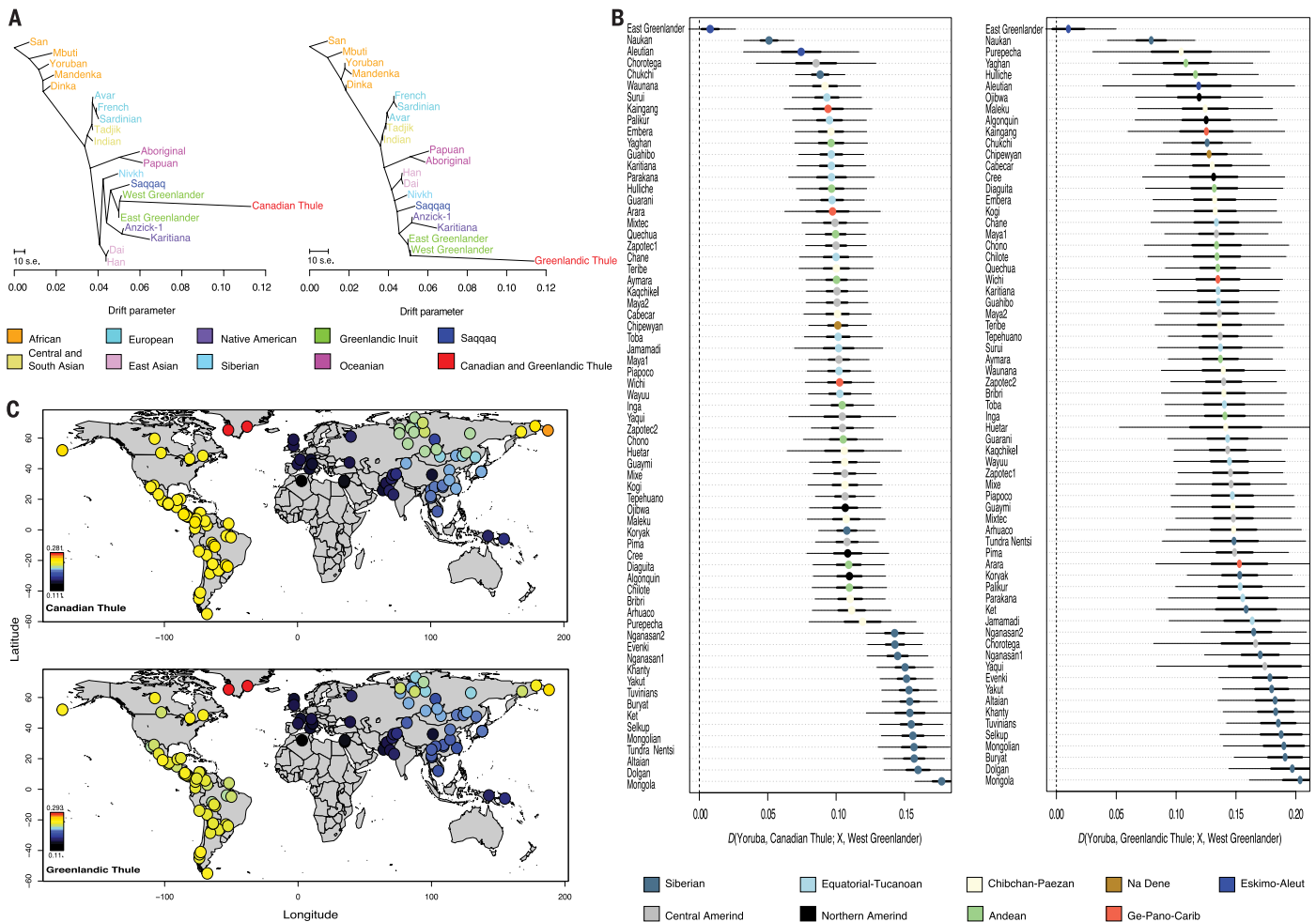


Fig. 4. Genetic affinities of the Neo-Eskimo Thule. (A) Sequencing data-based maximum likelihood trees constructed with *TreeMix* (51) with the high-coverage Saqqaq (26), Canadian Thule, and Greenlandic Thule data sets, and 17 present-day and 2 ancient populations. The scale bar represents 10 times the average standard error (s.e.) of the values in the covariance matrix. Residual matrices are shown in fig. S13, A and B. (B) SNP chip data-based D -statistic

tests of the form $D(\text{Yoruba, Thule}; X, \text{West Greenlander})$, as in Fig. 3. Canadian and Greenlandic Thule (left and right panels, respectively) are significantly (no overlap at 3 standard errors) closer to present-day West Greenlandic Inuit than to other worldwide present-day populations. Similar results are observed with East Greenlandic Inuit in place of West Greenlandic Inuit (fig. S14C). (C) Heat maps of the SNP chip data-based statistic $f_3(\text{Yoruba}; \text{Thule}, X)$, as in Fig. 3.

continuum of the same single ancestral population (Fig. 2, A and B, scenario 1). Present-day populations that are genetically closely related to the Paleo-Eskimos include the Greenlandic Inuit, Aleutian Islanders, and far-east Siberians (Fig. 3C and fig. S10E).

We additionally tested the claim that Saqqaq and Na Dene speakers were part of the same expansion into the Americas (28) by including present-day Athabascans, who represent distinct early branches of Native Americans (50), in the *TreeMix* (51) analysis. The maximum likelihood tree places the Athabascans as a sister clade to Karitiana and Anzick-1 (fig. S11A). Similarly, using SNP chip data from select Old and New World populations, masked for European admixture, we observe that the high-coverage Saqqaq individual forms a clade with the far-east Siberian Koryaks instead of with the Chipewyan, another Na Dene population (28) that groups with the South American Karitiana (fig. S11B). Outgroup

f_3 -statistics (52, 53) and D -statistics (52, 54) show that the high-coverage Saqqaq individual is closer to Greenlandic Inuit than to the Na Dene speakers (fig. S12, A to C). Furthermore, the lack of support for the Saqqaq being closer to the Athabascans than to Karitiana (fig. S12B) is incompatible with a scenario where Saqqaq and Na Dene speakers share a fraction of their ancestries through a secondary Asian stream (28). Overall, our results support the Paleo-Eskimo migration into the Americas as being separate from that of the Na Dene Native Americans.

Genetic affiliations of Neo-Eskimos

Greenlandic and Canadian Neo-Eskimo Thule, and present-day Greenlandic Inuit, form a clade in the maximum likelihood trees (Fig. 4A), even under admixture scenarios generated with *TreeMix* (51) (fig. S13, A and B). This supports genetic continuity over the last ~1000 years between these populations, which is also evident by the shared

mtDNA haplogroups (hgs A2a, A2b, and D3a2a) between them (supplementary text S4 and tables S1 and S9A). Furthermore, outgroup f_3 -statistics (52, 53) and D -statistics (52, 54) demonstrate that both Greenlandic and Canadian Thule are closer to present-day Inuit than to other sampled present-day populations or the high-coverage Saqqaq individual (Fig. 4, B and C, and fig. S14, A to C). These results are in agreement with the archaeological literature which suggests that present-day Greenlandic Inuit are direct descendants of the Thule (9, 56–58) (Fig. 2B, scenario 5).

We additionally analyzed five ancient individuals dated to the 6th to 7th century CE and associated with the Siberian Birnirk culture, which is part of the Neo-Eskimo tradition and may be one of the cultural ancestors of the Thule (59–61). Evidence from both mitochondrial typing (hg A2a) (tables S1 and S9A) and nuclear markers (fig. S15, A to D) reveals that these individuals are genetically closely related to present-day Greenlandic

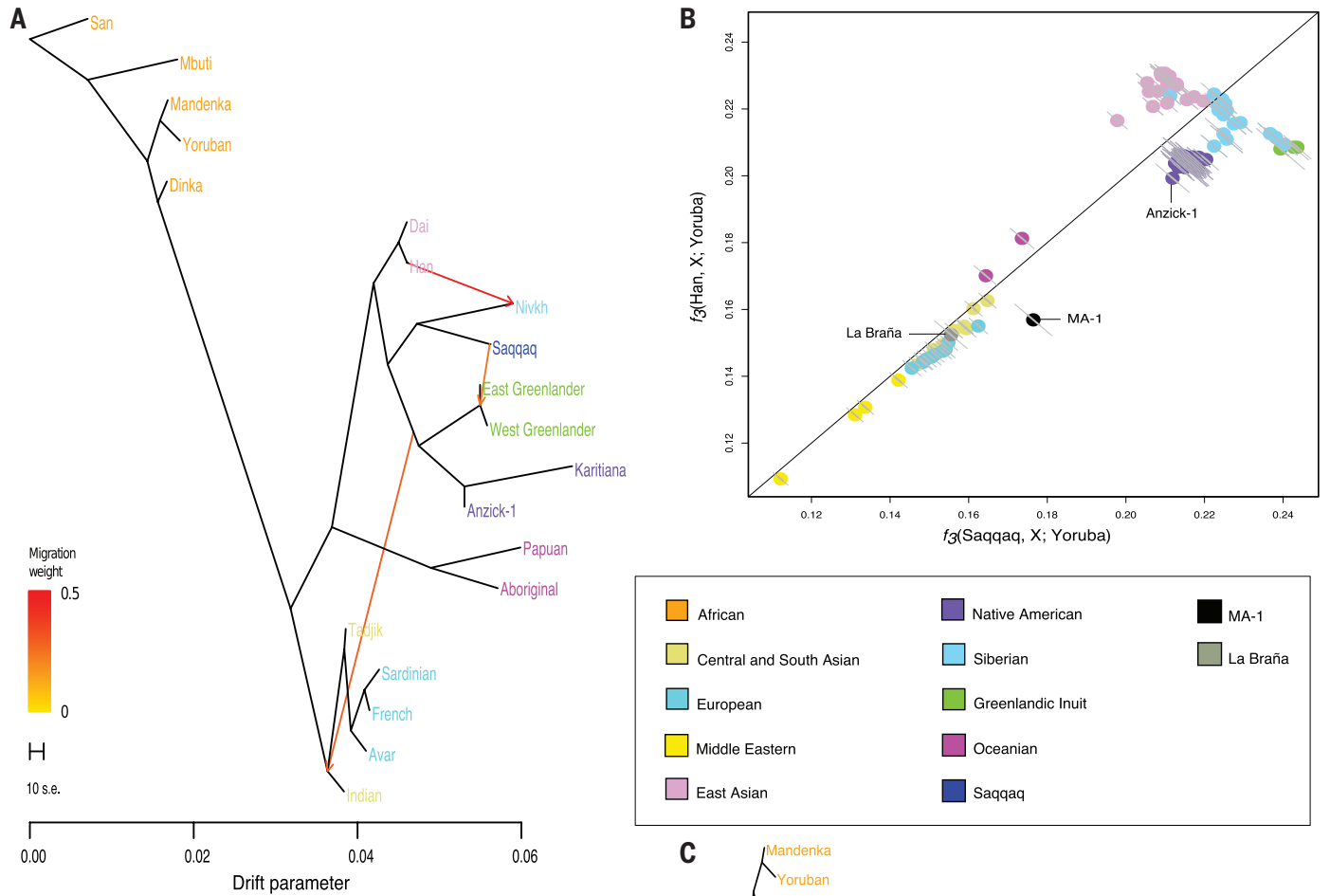


Fig. 5. Admixture signals in Paleo-Eskimos and Greenlandic Inuit. (A) Admixture graph (number of migration edges, $m = 3$) constructed with *TreeMix* (51), with the high-coverage Saqqaq (26), 17 present-day individuals, and two other ancient individuals. The scale bar represents 10 times the average standard error (s.e.) of the values in the covariance matrix, and the migration weight represents the fraction of ancestry derived from the migration edge. Migration edges are observed between the Paleo-Eskimos and Greenlandic Inuit, shown here as gene flow from the high-coverage Saqqaq to the root of East and West Greenlandic Inuit, although gene flow in the other direction is also observed (table S13). Admixture graphs with other Paleo-Eskimo and Neo-Eskimo populations, different numbers of migration edges, and residual matrices are shown in figs. S8, A, C, and D; S13, A and B; and S15A) **(B)** Biplot of SNP chip data-based statistic $f_3(\text{Saqqaq, X; Yoruba})$ versus $f_3(\text{Han, X; Yoruba})$, where X represents present-day worldwide non-African populations from (28). Thick and thin errors bars represent 1 and 3 standard errors of the f_3 -statistics, respectively. Western Eurasian populations (Europeans and South and Central Asians) are shifted toward the high-coverage Saqqaq compared to the Han Chinese. La Braña 1 was included in the analysis to evaluate potential ancient DNA bias between the Saqqaq and MA-1 data sets. **(C)** Sequencing data-based admixture graph with 17 present-day and 4 ancient individuals. A known migration edge is inferred from MA-1 to the root of Native Americans and Inuit, but this gene flow event excludes the high-coverage Saqqaq individual. Admixture graphs with different number of migration edges and residual matrices are shown in fig. S20, and bootstrapping results are shown in table S13. See supplementary text S5 for note on the migration edge from Saqqaq into MA-1.

Inuit, providing the first genetic evidence of an Old World population that was not only a cultural precursor of the Thule, but also either closely related to or a component of the ancestral Inuit gene pool (Fig. 2B, scenario 6). We also reassessed claims

that the Sadlermiut population from Southampton Island in the Hudson Bay region are remnants of the Dorset Paleo-Eskimo people on the basis of cultural similarities and mtDNA markers (33, 46, 62) (Fig. 2B, scenario 7). We typed 10

Sadlermiut individuals, dating to the 14th to 19th century CE, to mtDNA hgs A2b and D3a2a (supplementary text S4 and tables S1 and S9A), which are characteristic of the Thule/Inuit. Also, from their nuclear genome sequences, two of these

individuals (Canadian Thule) form a clade with present-day Greenlandic Inuit and not the high-coverage Saqqaq individual (Fig. 4A and fig. S13A). This implies that the Sadlermiut were either genetically derived from or closely related to the Thule rather than the Paleo-Eskimos (Fig. 2B, scenario 8).

Additionally, whether the Norse admixed with neighboring Dorset or Thule groups remains debated, even though no anthropological evidence supporting such admixture has been found (63). To address this hypothesis, we tested 34 Norse individuals from southern Greenland, across the time span of their occupation in the region, for matrilineal admixture with neighboring Paleo- and Neo-Eskimo populations (supplementary text S1). We found no New World-specific mitochondrial markers in these Norse samples, especially the Arctic-specific hgs A and D, suggesting that no detectable matrilineal gene flow occurred from the Dorset or Thule into the sampled Greenlandic Norse (supplementary text S4 and table S9, B and C).

Admixture signals in Paleo- and Neo-Eskimos

We further investigated the observed genetic affinity between present-day Greenlandic Inuit and Paleo-Eskimos. D -statistics (52, 54) and outgroup f_3 -statistics (52, 53) support the Paleo-Eskimos as being closer to Greenlandic Inuit than to other present-day New World populations (figs. S12A and S16, A and B), with the exception of the Aleutian Islanders, whose genetic proximity to the Inuit is evident in analyses from both sequencing data (fig. S9) and SNP chip data (28) and the Naukan who have been shown to possess Eskimo-Aleut ancestry as a result of back-migration of a related population (28). Maximum likelihood trees with migration edges inferred with *TreeMix* show evidence for admixture between Paleo-Eskimos and Greenlandic Inuit (Fig. 5A), mediated by the Neo-Eskimo groups that include the Canadian Thule, Greenlandic Thule, and Siberian Birnirk (figs. S8, A and C to D; S13, A and B; and S15A). In all the cases, this gene flow event is among the first few migration edges to be inferred by *TreeMix* (number of migration edges $m = 1$ to 4). Bootstrap support suggests that gene flow likely occurred in both directions between the Paleo- and Neo-Eskimo groups (table S13).

Although gene flow was also observed when the high-coverage Saqqaq individual was included, we sought to determine whether this was due to *TreeMix* being unable to distinguish between Saqqaq and Dorset as a result of their genetic similarity and if admixture might have actually occurred between Dorset and Neo-Eskimos. Therefore, we generated simulated data sets with varying levels of admixture (10 and 25%) between Dorset and Inuit in both directions, and determined whether a migration edge was observed in the *TreeMix* admixture graphs between the high-coverage Saqqaq individual and the Inuit in the absence of the Dorset (supplementary text S5). Simulated admixture from Dorset

to Inuit was detected by the analysis in the form of gene flow between Saqqaq and Inuit, but the reverse—that is, from Inuit to Dorset through gene flow involving Saqqaq and Inuit—was less likely (fig. S17, A and B, and table S13). Because our data show support for gene flow from the various Neo-Eskimo groups, including present-day Inuit, into the high-coverage Saqqaq individual, it is likely that the admixture involving Saqqaq is not an artifact and occurred from the Neo-Eskimo lineage into Saqqaq. We cannot, however, exclude the possibility of gene flow from Paleo-Eskimos into Neo-Eskimos as well, or that subsequent gene flow did not occur between the later Dorset phases and the Neo-Eskimo lineage (table S13).

Because the observed admixture involves the 4000-year-old Saqqaq individual, it implies that the meeting and intermixing of Paleo-Eskimo and Neo-Eskimo ancestors predates the first archaeological observations of their coexistence in the eastern Arctic by ~3000 years or earlier, since Thule groups entered eastern Canada and Greenland, previously occupied by the Late Dorset, only in the 12th or 13th century CE. This also suggests that the admixture is more likely to have occurred either in the Old World before the entry of the Neo-Eskimos into the Americas, or in Beringia, but not further east in the New World, because no archaeological evidence of a parallel existence of Paleo- and Neo-Eskimos around 4000 years ago or earlier has been documented in this region (Fig. 2B, scenario 9).

We also investigated the level of genetic contribution from the ~24,000-year-old Siberian boy from Mal'ta (MA-1) (53) into Paleo-Eskimos and Greenlandic Inuit. Pairwise outgroup f_3 -statistics (52, 53) show that sampled western Eurasians and MA-1 are slightly closer to the high-coverage Saqqaq than to the Han Chinese (Fig. 5B and fig. S18). To confirm that this genetic affinity between Saqqaq and MA-1 was not due to ancient DNA bias, we also included the ~7000-year-old La Braña 1 sample from Spain (64) in our analysis and found that it clustered close to present-day Europeans, hence confirming that our results were not skewed by ancient DNA attraction (Fig. 5B). *TreeMix* infers gene flow from the high-coverage Saqqaq into MA-1 and vice versa, the latter admixture edge being consistent with (65), but with low support to substantiate this signal and the inferred direction (Fig. 5C, table S13, and supplementary text S5).

In contrast, gene flow from MA-1 into the root of the clade comprising Native American populations (Karitiana and Anzick-1) and including the Greenlandic Inuit is detected with high bootstrap support, in agreement with (53) (Fig. 2B, scenario 10; Fig. 5C; and table S13). Additionally, D -statistics (52) and outgroup f_3 -statistics (52, 53) based on SNP chip data show that MA-1 is significantly (no overlap at 3 standard errors) closer to the Chipewyan than to the high-coverage Saqqaq (fig. S19), which is compatible with other results presented in this study that also reject a single-wave model for Saqqaq and Na Dene speakers. Overall, although there is evidence of genetic affinity between MA-1 and Saqqaq, we cannot

ascertain whether this is due to gene flow or shared ancestry between the two lineages. It is also possible that this affinity is a consequence of the aforementioned gene flow from Neo-Eskimos, who received MA-1 gene flow, into the Saqqaq lineage.

Discussion

We overcome the difficulties of studying the peopling of the Arctic by including an extensive collection of Paleo-Eskimo remains for both ancient DNA and radiocarbon analyses. We have shown that Paleo-Eskimos likely represent a single migration pulse into North America from Siberia; separate from the migration events giving rise to Native Americans and Inuit. However, while being genetically distinct from other New World populations, Paleo-Eskimos are still more closely related to these populations than to non-New World populations, which is in agreement with a single ancestral population giving rise to many subpopulations and possibly many migration pulses into the Americas, as suggested by the Beringian standstill model (66) and a three-stage colonization model (67). Moreover, although our data are in agreement with Reich *et al.* (28), we find no support for Saqqaq or the rest of the Paleo-Eskimo tradition being a part of one of the two waves of Native American ancestors entering the more southern regions of the Americas. Therefore, an additional Paleo-Eskimo migration wave should be added to the three-wave hypothesis in explaining the peopling of the Americas (28).

Furthermore, Paleo-Eskimo and Inuit peoples appear to have occupied the New World Arctic for more than 4000 years, with only a single population replacement (Thule) less than 700 years ago. In contrast with the dynamic responses of the Thule people to climate change (21, 68, 69), Siberian iron trade (70), and Norse contact (16), the 4000-year Paleo-Eskimo period presents a single tradition of continuous technological and social development, including geographical displacements and periods of relative stability punctuated by episodes of rapid change (20). The long-term continuity of the Paleo-Eskimo population and its culture is especially striking given the climatic and ecological cycles over 4000 years—from warm hypsithermal to cold sub-boreal through the early medieval warm event, as well as changes in sea ice distribution and in animal population cycles and distribution (13). In light of this, Paleo-Eskimo survival must be due to remarkable resilience among dispersed local groups with the ability to shift their small population units to new areas when their homes became untenable, like the complete depopulation of Greenland and the abandonment of the Canadian High Arctic between ~1 to 700 CE (9). Such events argue for the reformulation of the original “core area” hypothesis to a network of regional “core areas” that served as demographic reservoirs for repopulating areas abandoned as a result of climate change, animal population crashes, or human overhunting.

This study also contributes to the long-standing debate about the Dorset-Thule transition. New

series of radiocarbon dates suggest temporal overlap between the Dorset and the Thule that lasted between 50 and 200 years, with geographical coexistence in some areas (14, 16, 71–75), whereas an earlier reassessment of the eastern Arctic radiocarbon dates suggested that Dorset had disappeared from the eastern Arctic more than 200 years prior to Thule entering the eastern Arctic and thus the two groups never met (12, 76). Although we cannot preclude later gene flow between the Dorset and the Thule (that is, subsequent to the more ancient gene flow that occurred at least 4000 years ago), the contrasting genetic and cultural affinities of the Sadlermiut individuals present a conundrum. This culture that went extinct in 1903 CE from European disease has long been considered Thule-acculturated Dorset people, likely due to intermarriage (33, 77, 78); however, genetic evidence from this study suggests that they were Thule people who had somehow acquired Dorset stone technology (12, 79). Hence, if the acculturation evident among the Sadlermiut was not a result of intermarriage, what social mechanisms resulted in genetic isolation but allowed for cultural exchange? Similar questions can be raised with regard to lack of Thule or Dorset matrilineal gene flow with the Greenlandic Norse (75).

Our study contrasts with previous population-level genetic studies, such as those focusing on the introduction of agriculture in Europe (Neolithization), which found that population movements instigated changes in culture and subsistence strategies (65, 80–82). Paleo-Eskimo technological innovations seem to have occurred solely by the movement of ideas within a single resident population. Hence, our findings suggest that caution is required when using cultural similarities and differences as proxies for population movements and migrations into new and dramatically different environments.

Methods

DNA from 169 ancient human bone, teeth, and hair samples from Arctic Siberia, Alaska, Canada, and Greenland was extracted and targeted for haplogroup diagnostic mtDNA markers, while a subset of 26 samples was converted into Illumina libraries and sequenced, using standard laboratory procedures (supplementary text S3). Two present-day Greenlandic Inuit, two Nivkhs, one Aleutian Islander, and two Athabascans were genome sequenced with no objections from The National Committee on Health Research Ethics, Denmark (H-3-2012-FSP21) (supplementary text S2). Twenty-seven ancient samples were radiocarbon dated, of which 25 dates were corrected for marine reservoir offset (supplementary text S2). Mitochondrial DNA contamination estimates were computed as noted in supplementary text S4. Error rate analysis, DNA damage analysis, multidimensional scaling analysis on SNP chip and sequencing data, NGSadmix analysis, ABBA-BABA tests on sequencing data, D -statistics and f_3 -statistics tests on SNP chip and sequencing data, *TreeMix* analysis on SNP chip and sequencing data, neighbor-joining analysis,

and ancestry painting of the Aleutian genome were performed as described in supplementary text S5.

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SUPPLEMENTARY MATERIALS

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